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A STUDY OF THE EOCENE
CONDYLARTHAN MAMMAL
HYOPSODUS

(WITH 13 PLATES)

By

C. LEWIS GAZIN

Senior Scientist, Department of Paleobiology
United States National Museum
Smithsonian Institution



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By

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Smithsonian Institution*

(WITH 13 PLATES)

INTRODUCTION

UNDOUBTEDLY THE MOST CHARACTERISTIC MAMMAL that existed during Eocene time in North America was the small condylarth *Hyopsodus*. It is represented in the earliest to essentially the latest horizons of this period, but is not recognized surely as such in the preceding Paleocene, and evidently became extinct before the beginning of the Oligocene. Significantly, moreover, remains, such as jaw fragments and teeth, representing various species, while but sparsely encountered in later Eocene horizons, demonstrate that *Hyopsodus* was one of the most common of the land mammals in the early Eocene and quite the most common in the middle Eocene. Nevertheless, well-preserved skulls or comprehensive portions of skeletons are exceedingly rare.

Hyopsodus was first described (Leidy, 1870) nearly a hundred years ago and closely followed the earliest of the fossil mammal genera to be named from the Eocene of North America; preceded only by *Anchippodus* (1868) from the New Jersey marls, and by *Omomys* (1869) and *Patriofelis* (1870) from the Bridger formation of Wyoming. In its subsequent history of investigation, interpreta-

¹ Study of early Tertiary mammals was aided by grant G10686 from the National Science Foundation.

tion of its relationships has been nearly as varied as that for its partially contemporary *Meniscotherium*, and has been considered related to such distinctive groups as artiodactyls, perissodactyls, proboscideans, and notoungulates, as well as allocated to the Primates, Insectivora, Condylarthra, and Cope's Bunotheria.

The only prior comprehensive study of *Hyopsodus* was that by Matthew in 1909(b), as a part of a monograph on Bridger materials, continued in 1915(b) to include the earlier Eocene collections. Mention may also be made of brief reviews by Osborn in 1902 and Loomis in 1905, and a statistical interpretation by Olson and Miller in 1958, to be discussed more fully in the following pages. The writer's interest in the genus was spurred largely by newer materials of unusual quality and better documented collections, permitting a more detailed study and a much needed taxonomic revision of some 31 species names that have been applied to the genus.

ACKNOWLEDGMENTS

The rather large collections of *Hyopsodus* material, particularly from the Bridger formation, in the U. S. National Museum, were the basis for the present study; nevertheless, various universities and other museums aided immeasurably in permitting me to extend investigations to their collections and to borrow type-materials and certain other specimens for illustration and further study in Washington.

The American Museum of Natural History (AM), through the kindness of Drs. Edwin H. Colbert, Bobb Schaeffer, and Malcolm C. McKenna, has permitted me to study *Hyopsodus* and related materials in the various Eocene collections, to borrow certain specimens having associated skeletal material, and has allowed me to re-illustrate the several type-specimens in these collections. Drs. Elwyn L. Simons and James A. Hopson permitted me to review *Hyopsodus* material in a newly acquired Yale collection (YPM) from Lysitean beds in the Bighorn Basin, and to borrow a Marsh type for illustration. Also Dr. Peter Robinson while at Yale sent me for study the upper Eocene specimens of *Hyopsodus* found in the Marsh collection. Information on *Hyopsodus* was included in my study of faunal associations in the Eocene materials from the De Beque formation through the courtesy of Drs. Rainer Zangerl, Robert H. Denison, and William D. Turnbull at the Field Museum of Natural History. Data on horizons for localities yielding these latter materials were furnished by Mr. Bryan Patterson, formerly at that institution. Dr. Glenn L. Jepsen graciously made it possible for me to review the *Hyopsodus* materials at Prince-

ton University, in collections from the early Eocene of the Bighorn Basin, made by his parties. Dr. Albert E. Wood made arrangements for me to study the Lysitean materials at Amherst (AC) and to borrow Loomis' types for illustration. The upper Eocene materials in the Carnegie Museum from the Badwater area in the Wind River Basin and the Three Forks area of Montana were made available for my study through the kindness of Drs. Craig C. Black and Mary R. Dawson. Much appreciated loans of other type-specimens for re-illustrating were graciously made by Dr. Alfred M. Bailey, director of the Denver Museum of Natural History (DMNH), through the kind offices of Dr. G. Edward Lewis of the U. S. Geological Survey; Dr. Donald E. Savage of the University of California (UC); and Mr. Bryan Patterson of the Museum of Comparative Zoology (MCZ). Dr. Dale A. Russell of the National Museum of Canada (NMC) very kindly prepared a cast for me of a type preserved in Ottawa.

Mr. Lawrence B. Isham, staff illustrator for the Department of Paleobiology in the U. S. National Museum (USNM), made the pencil shaded drawings for the plates accompanying this report. He also drafted the frequency distribution charts and restorations included with the text.

HISTORY OF INVESTIGATION

Discovery and description.—The original description of *Hyopsodus* was made by Leidy in 1870. The type of the first named species, *H. paulus*, is a portion of a lower jaw with much worn molars, found near Fort Bridger² and sent to Leidy by F. V. Hayden. In the following year Marsh (1871) described a lower jaw portion with the better part of three, somewhat less worn, anterior cheek teeth as *Hyopsodus gracilis*. According to Marsh, "The specimens representing this species at present were found by the writer at Grizzly Buttes, Wyoming." Only one specimen, however, was described. It is interesting to note that Leidy (1872b), realizing that Marsh's "*H.*" *gracilis* did not belong to *Hyopsodus*, gave a new form, *Microsyops*, the species name *gracilis* because he believed that Marsh's "*H.*" *gracilis* was the same. Cope (1872), however, was more nearly correct in referring Marsh's species to *Notharctus*, although in 1873 he followed Leidy in referring it to *Microsyops*. "*Hyopsodus*" *gracilis* was subsequently made the type of the primate *Smilodectes* by Wortman (1903, vol. 16, p. 362).

² According to Leidy, but according to Matthew (1909b, p. 518) the type came from Church Buttes. This no doubt follows from Hayden's mention of collecting near Church Buttes on Sept. 10th and 11th, 1870 (Hayden, 1872, p. 41).

A second form described by Marsh (1872) as being near *Hyopsodus*, *Stenacodon rarus*, based on a third lower molar from near Henrys Fork, he later (1894) considered as being possibly allied to the artiodactyl *Helohyus*. Matthew (1899) tentatively retained it in this implied relationship, but both Osborn (1902) and Loomis (1905) regarded it as representing *Hyopsodus*. The specimen has since been lost.

In 1873, Cope described *Hyopsodus vicarius*, as a species of *Microsops* representing "an animal considerably smaller than the *Hyopsodus paulus*." The species was defined from two jaw fragments, one exhibiting the anterior molar and the other the second and third molars, from "the Badlands of Cottonwood Creek" (lower Bridger). The same year, but evidently somewhat later, Leidy described *Hyopsodus minusculus* from a maxillary portion discovered by Dr. Carter in the buttes of Dry Creek (also lower Bridger). This also was characterized by its small size in comparison with *Hyopsodus paulus*. In 1875, Cope realized that his *M. vicarius* was *Hyopsodus* and pointed out that Leidy's *H. minusculus* was a synonym. Matthew (1909b) later resolved this somewhat differently, regarding slightly larger *H. vicarius* as a small variant of *H. paulus* and retaining *H. minusculus* as the name for the distinctly small contemporary of *H. paulus*.

Cope (1874), with attention now turned to the early Eocene of New Mexico, described *H. miticulus* as a species of *Esthonyx*, from lower jaw portions of three or four individuals. In 1875, while recognizing that his "*Esthonyx*" *miticulus* belonged to *Hyopsodus*, he described a second species from these beds, somewhat larger *H. mentalis*, but as a species of *Antiacodon* which he later included under *Sarcolemur*. The type of this was a lower jaw with the first two molars. The materials of these two species were figured by Cope in 1877 but do not now appear to be extant. They were not with the associated materials in the U. S. National Museum at the time (1907) the type-catalog was prepared.

A third Marsh (1875) name pertinent to this review, *Lemuravus distans*, was based on skeletal portions described as found ". . . in the lower Eocene of Wyoming, . . ." distinct from *Hyopsodus* in a mistaken interpretation of the dental formula of the latter. He further proposed the family name Lemuravidae to include both *Hyopsodus* and *Lemuravus*. The genus was regarded as a synonym of *Hyopsodus* by Osborn (1902), Loomis (1905), and Matthew (1909b), and the species identical to *Hyopsodus paulus* by Matthew (1909b).

The first apparent indication that the range of *Hyopsodus* extended into the upper Eocene was inclusion of the name "*Hyopsodus gracilis*" in a list of the fauna of the Uinta beds by Clarence King in 1878. This list was evidently furnished by Marsh, but there is no indication of the specimen or specimens referred to. Therefore, it is not known whether a true primate, as implied, or *Hyopsodus* was involved, presumably the latter, inasmuch as *Smilodectes* does not occur so high and there are three *Hyopsodus* specimens in the Yale collections from the Uinta, cataloged as having been collected by Chew and Forshey in 1877 at "White River, Utah." King's listing, however, accounts for the citing of "*Hyopsodus gracilis*" in the Uinta faunas by later workers, including Scott (1890), Osborn (1895), Matthew (1899, 1909a), and Hay (1902).

Apparently the first mention of *Hyopsodus* in the early Eocene of Wyoming was Cope's preliminary report (1880a) on a collection from the Wind River beds made by Wortman the same year. In a later note (1880b) he described as coming from these beds a jaw which he made the type of "*Hyopsodus*" *speirianus*. In 1881 he transferred this species to *Microsyops* and in 1915 Matthew made it the type of *Haplomylus*. Matthew also showed that the specimen was from the Bighorn Basin and not the Wind River. Unquestionable material of *Hyopsodus* in Wortman's Wind River collection, however, was referred by Cope (1881) to *H. paulus* and *H. vicarius*.

The first new name to be applied to material of *Hyopsodus* from the early Eocene of Wyoming, Cope's *Hyopsodus lemoinianus* (1882a, p. 149), was based on a lower jaw from the Bighorn Basin, represented in all by "nine more or less fragmentary mandibles." In this same report, he referred eleven mandibles from the Bighorn Basin to the New Mexican Paleocene form *Phenacodus zuniensis* (a synonym of *Tricentes subtrigonus*). These were the basis in 1884 for his *Hyopsodus powellianus*. Of further interest in the 1882(a) report, Cope described as new *Phenacodus laticuneus*, to which later in the year (1882b) he gave the new generic name *Diacodexis*. Matthew (1899) indicated that the type-material consisted of upper premolars of *Hyracotherium* and upper and lower molars of *Hyopsodus* and referred the species to the latter genus. However, Sinclair (1914) discovered that the lower molar (M_3) belonged to a dichobunid artiodactyl, and since Cope's diagnosis (1882a, key, p. 179) was based essentially on this tooth, he regarded it as the only portion of the type to which the name is applicable, removing the species from *Hyopsodus*. Finally, Cope (1882c) described as new *Hyopsodus*

acolytus based on materials from the Paleocene of New Mexico, evidently the Torrejon horizon. He later (1888) included it in *Mioclaenus* and Matthew in his revision of 1937 included it in *Ellipsodon*.

Lydekker (1885a), in a review of *Microchoerus*, considered that *Hyopsodus* was a synonym. This allocation seems to have been ignored, no doubt because his outline of the characters of *Microchoerus*, together with the illustrations of the teeth, showed the two forms to be quite unlike. Apparently the first direct application of the generic name *Hyopsodus* to a European form was Rüttimeyer's (1891) "*Hyopsodus*" *jurensis*, based on two upper teeth from the Swiss Eocene. Schlosser (1894) noted the error of Rüttimeyer's assignment and regarded the form as a dichobunid artiodactyl. Stehlin (1906) further showed "*Hyopsodus*" *jurensis* to be a synonym of *Mouillacitherium cartieri*.

In 1902, Osborn reviewed the species of *Hyopsodus*, along with the true primates of the Eocene, but in part confused with them the artiodactyls *Microsus* and *Antiacodon*. Among the forms named as new, *Hyopsodus wortmani* was based on a figured maxilla and jaw of the smaller Wind River species that Cope (1881) had referred to *H. vicarius*. *Hyopsodus marshi*, a relatively large form, was described from maxillary portions found in the upper Bridger and the name *Hyopsodus uintensis* was given to the upper Eocene form occurring in the Uinta beds. The three specimens mentioned for the latter species were collected in 1895 from the upper or "C" horizon and evidently comprise the material referred to by Matthew as *Hyopsodus*, sp. in his 1899 list of the Uinta fauna. It may be noted, moreover, that Osborn (1902) first figured the Washakie Basin skull as *Hyopsodus paulus*. This illustration has been repeated in nearly every general textbook treatment since then.

A second review of the species of *Hyopsodus* was made by Loomis in 1905, but limited to consideration of the early Eocene or Wasatchian forms as represented in Amherst College collections from the Bighorn and Wind River Basins. Included in the discussion are the species *H. miticulus*, *H. lemoinianus*, *H. powellianus*, "*H.*" *laticuneus*, and *H. wortmani*. He described as new *H. simplex* from the Gray Bull beds, and *H. minor*, *H. browni*, and *H. jacksoni* from the Lysite beds of the Wind River Basin. The name *Hyopsodus lawsoni* beneath his figure 8 and in the table (op. cit., p. 424), not otherwise formally proposed, is clearly an error (lapsus memoriae), inasmuch as the figure and tabular information conform precisely with the text description of *H. jacksoni*.

Clearly the most critical and detailed prior treatment of *Hyopsodus* was Matthew's (1909b) revision of the Bridger forms. In this he brought out details of the appendicular skeleton, so far as known at that time, as well as further information on the skull. It may be noted, however, that Osborn, Scott, and Speir described the pelvis and femur of *Hyopsodus* as early as 1878. Matthew's preference for *Hyopsodus minusculus* instead of *H. vicarius* for the smaller of the two lower Bridger forms has been cited. He (1909b) described as new *H. despiciens* based on a skull from high in the upper Bridger (D) and referred to it the Washakie Basin skull that Osborn had cited as *H. paulus*. A smaller species, *H. lepidus*, was described as new from a lower horizon (C) in the upper Bridger. He indicated, moreover, a phylogenetic arrangement for the Bridger species which seems reasonable except for the equivocal position of "*Hyopsodus paulus vicarius*."

In 1915(b), Matthew extended his revision of *Hyopsodus* to include the lower Eocene or Wasatchian forms. At this time the new genus *Haplomylus* was proposed for the rather distinctive "*Hyopsodus*" *speirianus* from the lowest of the Gray Bull beds. Loomis' small *Hyopsodus simplex* was considered valid for an early Gray Bull or Sand Coulee form, and the ranges of Cope's New Mexican species *H. miticulus* and *H. mentalis* were regarded as extending to the Gray Bull and Lost Cabin horizons, respectively, of the Wyoming Eocene. *H. lemoinianus* was placed in synonymy with *H. mentalis*. For the smallest of the three Lost Cabin forms recognized Matthew retained Osborn's *H. wortmani*, and for the largest he proposed the new name *H. walcottianus*. Matthew considered that the Lysite forms were, in general, intermediate in character between those of the Gray Bull and those of the Lost Cabin, and the smallest of the Lysite forms, Loomis' *H. minor*, he regarded as a subspecies of *H. wortmani*. For the form of intermediate size he proposed the new subspecies *H. mentalis lysitensis*, and for the largest he considered that Cope's *H. powellianus* applied properly for the Bighorn Basin Lysite, but that in the Wind River Basin Lysite a somewhat smaller variant was represented. For the latter he used Loomis' name *H. browni* as a subspecies of *H. powellianus* and included as synonyms Loomis' *H. jacksoni* and *H. lawsoni*. It should be noted that the Wasatchian horizon represented by the type of Cope's *H. powellianus*, as well as of *H. lemoinianus*, is not certainly known.

A second supposed occurrence of *Hyopsodus* in the Eocene of Europe was reported by Teilhard de Chardin and Fraipont in 1921. The specimen, a lower molar tooth, is from the Sparnacian at Vinal-

mont in Belgium. There are various references in the literature to this occurrence but there does not appear to have been any critical re-examination reported, other than that of Teilhard de Chardin in 1922. Examination of the illustrations, as well as review of the description furnished, leads me to suspect that the relationship is not close.

While visiting the United States in 1925, Abel, together with Harold Cook, described (1925, p. 33) as new the species *Hyopsodus markmani*. The material consisted of a maxilla and jaw fragment of one individual in a collection of "early Eocene" remains "from a small and isolated spot in Colorado, . . ." The remarkably small "M¹" described is clearly a Dp⁴. There does not appear to have been any further report on the associated fauna. The occurrence, in Moffat County, Colorado, is now considered to be late Bridgerian in age.

A second species of *Hyopsodus* named on material from the upper Eocene, distinctly larger than *H. uintensis*, was described by Russell and Wickenden in 1933 (see also Russell, L. S., 1965). The form, *H. fastigatus*, was based on a lower molar from the Swift Current beds in Saskatchewan. Three other lower molars from the same beds were cited as paratypes, and a broken upper molar regarded as representing a somewhat smaller species. The associated fauna listed is clearly Uintan in age.

Also from the upper Eocene, *Hyopsodus egressus* was named by Stock (1934) from the Tapo Ranch locality in the Sespe formation of southern California. In addition to the type lower jaw, four additional fragments were referred and three upper teeth were cited as paratypes. The material represents an artiodactyl rather than *Hyopsodus* and McKenna (1959) proposed the new generic name *Tapochoeurus* for this species, allocating it to the Dichobunidae.

Comparatively recent studies involving *Hyopsodus* in the Wind River Basin include a report by Denison (1937) on a small collection of mammalian materials from early Wasatchian beds, presumably the Indian Meadows formation, near the North Fork of the Wind River in the western part of the basin. Among the specimens he recognized *Hyopsodus simplex*, and to a somewhat distinctive jaw portion with the two posterior molars he gave the new name *Hyopsodus latidens*. New collections made from somewhat higher in the section, the type Lysite in the northeasterly part of the basin, justified a revision of the Lysite fauna by Kelley and Wood (1954). Their treatment of *Hyopsodus*, in part statistical, reduced to three the number of names applicable, recognizing *H. powellianus*, *H. mentalis*, and *H. minor* in decreasing size ranges, and discarding the subspecies arrangement

proposed by Matthew (1915b). Still higher in the section, White (1952) identified *H. powellianus* and *H. wortmani* in Lost Cabin beds of the Boysen Reservoir area, and in 1956(b) I recognized *Hyopsodus*, cf. *wintensis* in the upper Eocene fauna from the Hendry Ranch member of the Tepee Trail formation at Badwater, farther east in the basin.

Review of the late Paleocene and early Eocene mammalian faunas by Van Houten (1945) includes information on the geographic and geologic distribution of species of *Hyopsodus* during Wasatchian time, and among my recent studies (1952, 1962) involving *Hyopsodus* are the investigations of the Wasatchian faunas of southwestern Wyoming. In the latter six species of early Eocene *Hyopsodus* are recognized, but not more than three in any one assemblage, defined essentially on frequency distribution of size of teeth. *Hyopsodus* material from the same depositional basin but from an early Wasatchian horizon represented in the adjacent part of Colorado, was recognized by McKenna in 1960 to include *H. miticulus* and a new species *H. loomisi*. The latter was described in part as possessing primitive characters attributed to *H. simplex* of the Bighorn Basin but not actually exhibited in the type. A rather thoroughgoing statistical treatment of *Hyopsodus* was made by Olson and Miller (1958) as a part of a demonstration of principles and procedures for showing relationships of characters, or statistically defining the morphology of the organism. The results of this study, however, are not useful in delineating or defining the species as this was assumed to have been accomplished. Unfortunately, it would appear that some of the population samples used in this genus are not homogeneous.

More recently Gazin (1965) has discussed many features of the *Hyopsodus* skeleton, in comparisons made between *Meniscotherium* and other condylarths; a review which, together with the acquisition of better materials and the taxonomic confusion noted for *Hyopsodus*, prompted the present study.

Relationships.—Interpretations of *Hyopsodus* relationships were discussed by Matthew (1909b, p. 508), but a brief review of the history of these seems appropriate here, with interesting additional details and later conclusions.

Leidy (1870, pp. 109-110) in his original description of *Hyopsodus* considered it a "small pachydermous animal," and "an animal probably allied to the suilline family." Later (1872b, 1873), however, after having seen many more specimens he still regarded it as a small "pachyderm," but an odd-toed form, listing along with it such genera

as *Notharctus* and *Microsyops*, together with the true perissodactyls. Cope (1875) also considered the teeth of *Hyopsodus* to be perissodactyl in type, but listed it with a variety of small contemporary forms as *Incertae Sedis*.

The idea that *Hyopsodus* was a primate originated with Marsh in 1875 (pp. 239-240) when he referred *Hyopsodus* and his new *Lemuravus* (= *Hyopsodus*) to the Lemnurae under the Prosimia, and stated that *Hyopsodus* ". . . proves on investigation to belong to the Primates, and not to the Ungulates. This is shown by the close correspondence of the skeleton with that of the lemurs, and by the general structure of the skull." Possibly he was influenced more by the dental characters of the primate "*Hyopsodus*" (now *Smilodectes*) *gracilis*, which he thought were representative of *Hyopsodus*. On the other hand, the materials that he described as *Lemuravus distans* were actually of *Hyopsodus*.

Cope, nevertheless, remained skeptical of this direct ordinal assignment and in 1877 included *Hyopsodus* along with the pantolestids, notharctids, etc., in the Mesodonta, which he had proposed in 1876 as one of the suborders of his new Bunotheria, and regarded as intermediate between the Creodonta and Prosimiae. He felt, however, that further investigation was needed to determine the relations of the Prosimiae to the Bunotheria. In 1882(a) the Prosimiae were also included as a suborder of the Bunotheria. Cope's ordinal arrangement with regard to *Hyopsodus* was generally followed by only a few, such as Trouessart (1879) and Seeley (1886). Most authorities, including Schlosser (1887, 1902); Osborn, Scott, and Speir (1878); Matthew (1899); Osborn (1902); and Weber (1904) regarded *Hyopsodus* as a primate. Earle (1898), however, referred to the hyopsodontids as pseudo-lemurs.

Marie Pavlow (1887) was evidently the first to note the condylarthran affinities of *Hyopsodus*. In her study of the paleontological history of the ungulates, but without actual reference to the order she commented on the closeness of "*Protogonia*" (*Tetraclaenodon*) to *Hyopsodus paulus* which she evidently regarded as representing the same genus ("n'est autre chose"), and considered it as belonging in the Phenacodontidae. Cope (1887, p. 657) in reply to Pavlow stated that "nothing but the teeth of *Hyopsodus* are as yet known, so that its position is uncertain. It may be lemuroid or an artiodactyl." Schlosser (1903), however, was somewhat more emphatic in comment on a later (1900) part of Pavlow's ungulate study; with reference to *Hyopsodus* he stated, "ist ja ein Primate!"

In a study of the Eocene primates in the Marsh collection Wortman (1903) pointed out a number of reasons why *Hyopsodus* should not be regarded as a primate and considered that it was much more like the Insectivora. Such a relationship, it may be noted, was considered rather close in Cope's interpretations, as in 1876 (p. 88) he stated, "I cannot find characters by which to distinguish this division [Mesodonta] from the Insectivora as an order." Lydekker (1885b) considered Cope's *Hyopsodus vicarius* as decidedly insectivorine and Seeley (1886) was also unable to separate Mesodonta from Insectivora. Heilprin (1887) regarded the forms in the Mesodonta as so closely linked to the Insectivora that they are barely, if at all, separable. Most writers following Wortman's exposition, including Loomis (1905), Matthew (1909b), Osborn (1910, with the new suborder Hyopsodonta), Zittel et al. (1911, textbook), and Abel (1914), concurred in allocating *Hyopsodus* to the Insectivora. As late as 1914, however, Bolk in a discussion of the morphology of primate teeth included *Hyopsodus* among the primates, citing Osborn (1902) as authority.

Matthew (1915a, 1915b) has been generally credited with recognition of the condylarthran affinities of *Hyopsodus*, and indeed strongly leaned toward this interpretation in his 1909(b) study of the genus. It is not certain that he was aware of Pavlov's interpretation as I find no reference to it in his discussion; nevertheless, his rather satisfactory demonstration of this relationship was clearly the first. It is surprising that, in view of this detailed exposition, we find Abel as late as 1922 and Schlosser in 1923 (in Zittel et al.), while noting Matthew's work, still regarded *Hyopsodus* as an insectivore. Abel, nevertheless, as a result of his study with Cook in 1925 of *Hyopsodus markmani*, was convinced of the ungulate affinities of *Hyopsodus* and considered the ancestry of the equids to be in the Hyopsodontidae which, in 1926(a and b) Abel related to the Protoungulata (Condylarthra). Friant, as late as 1934(a and b), in a study of erinaceid molars, discussed *Hyopsodus*, and while noting classification successively in the Primates, Insectivora, and Condylarthra, regarded its position as uncertain. More recently, Simpson (1945) in his classification of the mammals, Romer (1945) in textbook treatment, and Lavocat (1958) in the "Traité de Paléontologie" have followed closely Matthew's interpretation.

Gregory (1920, p. 244), in a phylogenetic review of the vertebrates included in his study of the lachrymal bone, suggested that "every one of the specialized characters of the dentition of *Moeritherium* has

been derived from the far more primitive conditions in some such primitive procondylarth as *Hyopsodus walcottianus* . . ." enumerating the dental features of *Hyopsodus* which he regarded as suggesting such a potential relationship to the Proboscidea.

Further interesting sidelights in suggested hyopsodont relationships include Ameghino's (1906) reference of the notoungulate *Selenoconus* to the Hyopsodontidae, which he regarded as primate in affinities. The actual resemblance, from Ameghino's figures, does not appear very close. I am more impressed with resemblance of Casamayor condylarthran *Asmithwoodwardia* to *Hyopsodus*, which Paula Couto (1952) considered as belonging in the same subfamily; nevertheless certain features appear rather distinctive. Perhaps an even closer approach is made by the Casamayor *Oxybunotherium* which Pascual (1965) referred tentatively to the Didolodontidae.

GEOGRAPHIC AND GEOLOGIC OCCURRENCE

The known geographic occurrence of *Hyopsodus* is limited to the western or Rocky Mountain region of North America from Saskatchewan to New Mexico. The bulk of the material, however, comes from Wyoming, as it is here we have very widely distributed, evidently better known, and certainly more persistently prospected Eocene than elsewhere. Reported occurrences in the Eocene of Europe, as has been noted in preceding pages, are evidently not of *Hyopsodus*. While not actually represented in South America, some forms encountered in the early Tertiary of Argentina seem to be closely related.

Hyopsodus is of relatively common occurrence in the earliest horizons of the Eocene, as at Four Mile Creek in the Colorado extension of the Washakie Basin, at Bitter Creek on the east flank of the Rock Springs Uplift, and in the Sand Coulee level of the Gray Bull beds in the Big Horn Basin. It has not been recorded, however, from the latest Paleocene,^a such as the Buckman Hollow Clarkforkian on the western margin of the Green River Basin, nor in beds of this age in the Clark Fork Basin proper of the northwestern part of the Big Horn Basin.

^a A lower jaw of *Hyopsodus* which I understand was collected by a University of Wyoming field party in the Bison Basin, appears to be correctly identified, but if from this area must surely be derived from a remnant of Eocene on or near the rim of the basin, probably to the west or southwest, rather than from one of the earlier levels of Tiffanian Paleocene represented along the escarpment below the southerly rim of the basin.

While of universal occurrence in reasonably representative collections from Wasatchian and Bridgerian early and middle Eocene of Wyoming, Colorado, and Utah, and early Eocene of New Mexico, *Hyopsodus*' proportion of the mammalian population apparently increased during this interval. Although comparatively common in the earlier or Graybullian substage, as represented in the Big Horn Basin, it is evidently not as frequently encountered as, for example, *Hyracotherium* and is closely approached or possibly exceeded by certain other groups. In Lysitean and Lostcabinian portions of the Wasatch it appears to at least equal the horse, while surpassing other groups, but during early Bridgerian time and probably throughout the middle Eocene it very considerably exceeds representation of any other mammalian genus.

In later Eocene time there appears to have been a marked regression to a less abundant state, certainly so far as the Uinta formation is concerned. *Hyopsodus* has been found very sparingly in Uinta "B" at White River pocket in the Uinta Basin, in Uinta "C" at Myton pocket, and at localities labelled "White River, Utah" (Marsh Coll.). Nevertheless, as a result of renewed collecting by the Carnegie Museum, a better representation of *Hyopsodus* in upper Eocene time is noted for the Hendry Ranch beds on Badwater Creek. Several specimens, moreover, have been found at an upper Eocene locality near Three Forks, Montana, and from the Swift Current Creek beds in Saskatchewan. There is no record, however, of the occurrence of *Hyopsodus* in beds of undoubted Oligocene ⁴ age.

CLASSIFICATION

Of the approximately 31 species names that have been applied to the genus *Hyopsodus*, six, as discussed in foregoing pages, were erroneously referred to this genus, and among the 25 remaining, five were originally described under other generic names. Results of the present study suggest that about 12 species names may be regarded as valid. Five of these are recognized for the Wasatchian early Eocene, five for Bridgerian middle Eocene, and two for late Eocene Uintan time. The synonymy is indicated in the following chronological listing, showing also information on the occurrence of the probably valid types and the interpreted range for the species.

⁴ An upper molar of *Hyopsodus* from an isolated locality on the Beaver Divide, reported to be in the Beaver Divide conglomerate, adds another to the list of controversial occurrences in this area (see Gazin, 1955, p. 7). The tooth appears rather less typically upper Eocene than perhaps earlier.

Condylarthra Cope, 1881

Hyopsodontidae Trouessart, 1879⁵*Hyopsodus* Leidy, 1870

Synonyms.—(?) *Stenacodon* Marsh, 1872; *Lemuravus* Marsh, 1875.

Type-species.—*Hyopsodus paulus* Leidy.

Hyopsodus paulus Leidy, 1870

Synonyms.—(?) *Stenacodon rarus* Marsh, 1872; *Lemuravus distans* Marsh, 1875; *Hyopsodus vicarius* (Cope), 1873.

Type.—Right ramus of mandible, USNM 1176, with M₁–M₃ (pl. 7, fig. 4).

Horizon and locality.—Lower Bridger middle Eocene, near Fort Bridger, Bridger Basin, Wyoming.

Range.—Lower part of Bridger formation, Blacks Fork member, Wyoming.

Hyopsodus minusculus Leidy, 1873

Type.—Left maxilla, ANS (Academy Natural Sciences) 10259, with M¹–M³ and part of P⁴ (Leidy, 1873, pl. 27, fig. 5).

Horizon and locality.—Lower Bridger middle Eocene, "Buttes of Dry Creek," Bridger Basin, Wyoming.

Range.—Lower part of Bridger formation, Blacks Fork member, Bridger Basin, Wyoming. Green River formation, Powder Wash Occurrence, Uintah Co., Utah.

Hyopsodus miticulus (Cope), 1874

Synonyms.—*Hyopsodus mentalis* (Cope), 1875; *Hyopsodus lemoinianus* Cope, 1882a; *Hyopsodus simplex* Loomis, 1905; *Hyopsodus lysitensis* Matthew, 1915b; *Hyopsodus latidens* Denison, 1937.

Type.—Left ramus of mandible, USNM (type not in collections since before 1907), with M₁–M₃ (Cope, 1877, pl. 45, fig. 10).

Horizon and locality.—Wasatchian early Eocene, San Jose formation, San Juan Basin, New Mexico.

Range.—Wasatchian early Eocene, New Mexico, Wyoming, and Colorado.

Hyopsodus powellianus Cope, 1884

Synonyms.—*Hyopsodus browni* Loomis, 1905; *Hyopsodus jacksoni* Loomis, 1905; *Hyopsodus lawsoni* Loomis, 1905.

Type.—Right ramus of mandible, AM 4147, with M₁–M₃ (pl. 8, fig. 8).

Horizon and locality.—Wasatchian early Eocene, Willwood formation, Big Horn Basin, Wyoming.

Range.—Middle and possibly later Wasatchian early Eocene, Wyoming and Colorado.

Hyopsodus uintensis Osborn, 1902

Type.—Right maxilla, AM 2079, with M¹–M² and part of P⁴ and M³ (pl. 9, fig. 2).

⁵ The spelling and authority here used follows the International Code of Zoological Nomenclature adopted by the 15th International Congress of Zoology. Trouessart's "Hyopsodinae" of 1879 was the first usage derived from *Hyopsodus* in the family group. Current spelling is as specified in Example 30, Table 2, Part B, of Appendix D7.

Horizon and locality.—Upper or "C" horizon of Uinta formation, Uinta Basin, Utah.

Range.—Late Eocene Uintan of Uinta Basin, Utah, and Wind River Basin, Wyoming.

Hyopsodus wortmani Osborn, 1902

Synonym.—*Hyopsodus minor* Loomis, 1905

Type.—Portions of maxillae, premaxillae, and both rami of mandible, AM 4716, with I^2 , P^2 – M^3 , and P_3 – M_3 represented (pl. 9, figs. 7–9).

Horizon and locality.—Late Wasatchian early Eocene, Wind River Basin, Wyoming.

Range.—Middle and late (and early ?) Wasatchian early Eocene, Wyoming, Colorado, and possibly New Mexico.

Hyopsodus marshi Osborn, 1902

Type.—Right and left maxillae, AM 1706a, with P^2 – M^3 represented (pl. 9, fig. 1).

Horizon and locality.—Late Bridgerian middle Eocene, Bridger Basin, Wyoming.

Range.—Upper part of Bridger formation, middle Eocene, Bridger Basin, Wyoming.

Hyopsodus despiciens Matthew, 1909b

Synonym.—*Hyopsodus markmani* Abel and Cook, 1925

Type.—Skull and left ramus of mandible, AM 11877, with P^2 – M^3 and P_1 – M_3 represented (pl. 7, figs. 1, 2).

Horizon and locality.—Late Bridgerian middle Eocene, Bridger "D," Henry's Fork, Bridger Basin, Wyoming.

Range.—Late Bridgerian middle Eocene, Bridger "C" and "D," Bridger Basin, and "middle beds" Washakie formation, Washakie Basin, Wyoming, and Sand Wash Basin, Moffat Co., Colorado.

Hyopsodus lepidus Matthew, 1909b

Type.—Right maxilla and left ramus of mandible, AM 11900, with P^2 – M^3 (Matthew, 1909b, pl. 48, fig. 4) and P_1 – M_3 and part of P_2 represented (pl. 7, fig. 3).

Horizon and locality.—Late Bridgerian middle Eocene, Bridger "C," Henry's Fork, Bridger Basin, Wyoming.

Range.—Late Bridgerian middle Eocene, Bridger "C" and "D," Bridger Basin, Wyoming.

Hyopsodus walcottianus Matthew, 1915b

Type.—Portions of both maxillae, left premaxilla, both rami of mandible, AM 14654, with two upper incisors, P^2 – M^3 , part of M^3 , and P_2 – M_3 represented (pl. 8, figs. 1–3). Including also limb and hind foot material.

Horizon and locality.—Late Wasatchian early Eocene, Lost Cabin beds, Alkali Creek, Wind River Basin, Wyoming.

Range.—Late Wasatchian early Eocene, Wyoming and Colorado.

Hyopsodus fastigatus Russell and Wickenden, 1933

Type.—Left M_2 , NMC 8654 (pl. 9, fig. 3).

Horizon and locality.—Uintan late Eocene, near Swift Current, Saskatchewan, Canada.

Range.—Uintan late Eocene, Saskatchewan and Montana.

Hyopsodus loomisi McKenna, 1960

Type.—Right maxilla, UC 44781, with P²-M³ (pl. 9, fig. 4).

Horizon and locality.—Earliest Wasatchian early Eocene, Four Mile Creek, Washakie Basin, Moffat Co., Colorado.

Range.—Earliest Wasatchian early Eocene, Wyoming and Colorado.

Species of *Hyopsodus*, it has been found, are rather difficult for the most part to separate on characters available in teeth and jaws, other than size, particularly contemporaneous forms, or those within the same larger time stages of the Eocene. As Matthew (1909b, pp. 516-517) noted, however, there is an observable trend in time. With regard to the transition from Wasatchian to Bridgerian species he stated that "The teeth of the Bridger species as a whole, show but little advance over those of the Wind River; there is no general increase in size; the premolar crowns are usually somewhat more complicated and the roots more crowded, P₂ is normally one-rooted, excepting in one species, while it is, as far as I have seen, always two-rooted in the Wind River. In the Wasatch the premolars are always considerably more primitive, with simpler, more trenchant crowns, and less completely quadritubercular. In all formations, however, the larger species are more advanced in tooth structure."

While I am unable to corroborate the more complicated crowns of the Bridger *Hyopsodus* premolars, I note that in the upper series P² in the Bridger material is decidedly more triangular, looking somewhat more like P³ of the Wasatchian condition, and P³ of the Bridger materials has come to look a little more like P⁴. With regard to the lower premolars, P₂ is clearly two-rooted in the early Eocene, but in the Bridger the condition is highly variable and the roots may be divided or completely coalesced, but more often appear to be incompletely divided at the margin of the alveolus, and no doubt separated in depth. It seems rather general that the premolar series, above and below, is relatively shorter, or more crowded appearing in Bridger materials than in the earlier Eocene. I am unable to verify, however, the more advanced teeth of the larger species in all formations, although this may be true in the case of *H. marshi* and *H. fastigatus*.

Contrasted with the Bridgerian species, I note in the later Eocene materials a distinct trend toward a more nearly lophodont condition in the molars. In the upper molars the hypocone has become more distinctly separated from the protocone and shows a somewhat stronger union with the metaconule, a condition reminiscent of *Hyracotherium*, although less progressive in this respect. In the lower molars the crests are a little higher, the posterior crests from the protoconid and hypoconid slightly more oblique, and the anterior crest

from the protoconid in the second and third molar each shows a tendency to form a more nearly continuous crest with the hypoconulid and entoconid of the preceding molar. These features as they pertain to the lower teeth appear a little less demonstrable in some of the Uinta Basin specimens (probably Uinta "B") than in the larger materials of the more northerly occurrences.

The extremes may be observed in a comparison between early Graybullian *Hyopsodus loomisi* and Uintan *Hyopsodus fastigatus*. Nevertheless, through much of Wasatchian time and within the Bridgerian interval the amount and nature of intraspecific variation renders definition on morphological grounds infeasible for practical application. The relative abundance of materials in most instances, however, has lent itself well to statistical analysis, and the application of these procedures to size and proportions of teeth has produced rather interesting results. While various parameters have been tried, it has been found that using the length of the second lower molar gives representative results, which may be simply portrayed.

The possibility that recognition of more than one species at a single horizon or locality may represent dimorphism within the species seems remote, because there are some localities, where adequate material is at hand, as at Grizzly Buttes in the Bridger Basin, the frequency distribution in size of M_2 indicates but a single form. In other instances, three may be demonstrated, and where two only are indicated, there may well be a great disparity in numbers representing each.

Wasatchian species.—Directing attention first to the early Eocene we find that the oldest names used are Cope's *Hyopsodus miticulus* and *Hyopsodus mentalis*, applied to materials from the San Jose beds in the San Juan Basin of New Mexico. The types for these two do not now appear to be extant, but considering the measurements given by Cope (1877, pp. 151 and 149) of 4.0 and 4.4 mm., respectively, for the length of M_1 doubt may be entertained as to the probability that two forms are represented. Utilizing all of the San Juan Basin materials known to me, a display has been prepared (fig. 1) showing the frequency distribution for length of M_1 , with Cope's measurements superimposed. This shows an observed range of 3.5 to 4.5 mm. and the coefficient of variation is found to be close to 6.5. The display alone is rather convincing that but a single species is represented with the type for the oldest name, *H. miticulus*, essentially at the mean, and the type for the synonym, *H. mentalis*, comfortably within the range. A frequency distribution for length of M_2 (see tops of figs. 3 and 4), the parameter selected for comparison, using essentially the same

sample of *H. miticulus*, shows a slightly greater observed range of 3.8 to 5.0 mm., with the mean close to 4.4 mm., but the coefficient of variation, at about 6.2, is slightly less.

With reference to the classic sections of early Eocene in Wyoming, it is seen from comparison of frequency distributions for length of M_2 (fig. 2) that more than one species is represented in the higher levels, and that one of these evidently runs through from Gray Bull to Lost Cabin time with but a small shift in mean from 3.89 in the Gray Bull, 4.07 in the Lysite, to 4.18 mm. in the Lost Cabin, the latter two representing the typical sections in the Wind River Basin. These are a little under the mean of 4.41 mm. for the San Juan Basin material of *H. miticulus*, but it is reasonable to consider that the contemporary (in part) Wyoming form is the same species.

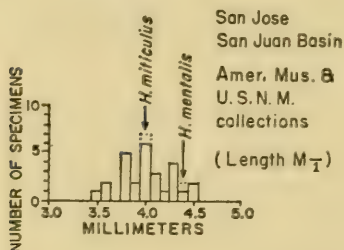


FIG. 1.—Frequency distribution for length of M_1 in *Hyopsodus miticulus* material from the San Jose formation in the San Juan Basin. Dotted rectangles represent positions for measurements of types furnished by Cope.

Direct comparison of the histogram for San Jose *H. miticulus* with those for the Lysitean stage in the Bighorn and Wind River Basins is shown in figure 3. The mode for the San Jose material appears rather closer to that for the Bighorn (Yale's Buffalo Basin collection) material than to that for the *H. miticulus* materials from the typical Lysite. The skewness exhibited in the Buffalo Basin representation, however, as well as the range for materials having M_2 less than 5 mm. is rather unusual, appearing suspiciously heterogeneous. Grouping these materials according to levels in the Buffalo Basin sequence, it was found that there is a certain uniformity within the median 200 feet of the Lysite zone with a clear separation between two species (see lower part of fig. 4) and a noticeable shift to the left for the upper approximately 115 feet (see middle part of fig. 4). Concurrent with the shift a much larger species appears in the representation of the hyopsodont population. The San Jose range and mean are more nearly coincident with those for the midsection of the Buffalo Basin Lysite, whereas the Wind River Lysitean *H. miticulus* display is more nearly conformable with that for the upper zone in the Buffalo Basin.

The comparison in figure 5 is between the San Jose histogram and the display for Lost Cabin age populations in both the Green River and Wind River Basins. The correspondence is somewhat better with *H. miticulus* materials from the Knight member of the Wasatch than

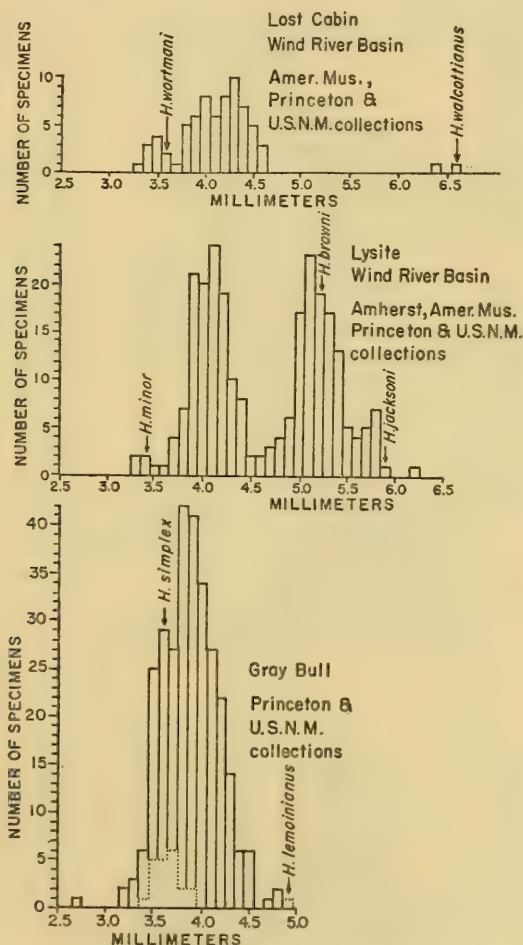


FIG. 2.—Comparison of frequency distributions for length of M_2 in *Hyopsodus* from typical sections of early Eocene or Wasatchian time in Wyoming. Names show positions of specimens that have been described as types. Dotted figure superimposed on Gray Bull distribution represents Sand Coulee alone, except for specimen designated *H. lemoianus* which is from an unknown horizon. The upper figure is interpreted as representing, left to right, *H. wortmani*, *H. miticulus*, and *H. walcottianus*; the central figure, *H. wortmani*, *H. miticulus*, and *H. powellianus*; and the lower figure essentially all *H. miticulus*.

with the typical Lost Cabin which seems to have a somewhat lower mean and range. Again, *H. miticulus*, in the latter, as in the upper zone of Buffalo Basin Lysite, is accompanied by a distinctly larger species, as well as a smaller form.

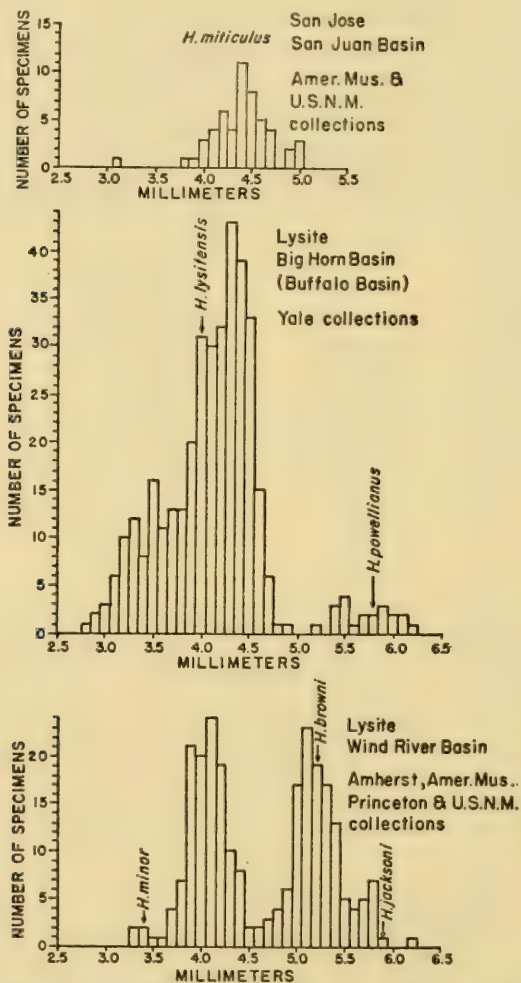


FIG. 3.—Comparison of frequency distributions for length of M_2 in *Hyopsodus* from Lysite horizons of the Wind River and Big Horn Basins with that for *H. miticulus* of the San Jose beds in the San Juan Basin. Names show positions of specimens that have been described as types. The central figure is interpreted as representing, left to right, *H. wortmani* and *H. miticulus* from mixed horizons, and *H. powellianus*; and the lower figure, *H. wortmani*, *H. miticulus*, and *H. powellianus* (subsp. *browni*?).

Among the names that appear synonymous with *H. miticulus* in the Wyoming basins are Loomis' *H. simplex* (pl. 9, fig. 10) of the Gray Bull and presumably Cope's *H. lemoianus* (pl. 9, fig. 5) based on a type thought to be from the Gray Bull. It seems unlikely that Cope collected from the Lost Cabin levels in the Bighorn Basin, but if *H. lemoianus* came from the Lysite zone, its length of M_2 again falls at

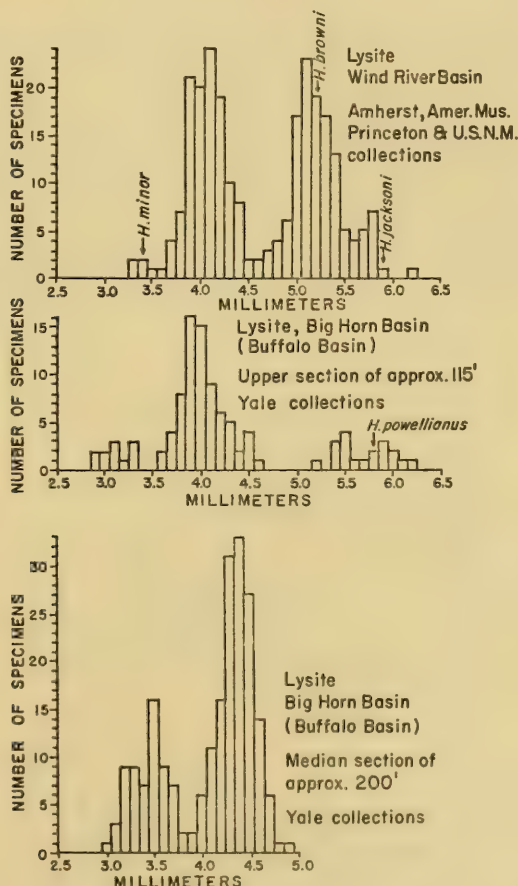


FIG. 4.—Comparison of frequency distributions for length of M_2 in *Hyopsodus* from the Lysite of the Wind River Basin with those for the middle and upper zones of the Lysite in the Big Horn Basin. Names show positions of specimens that have been described as types. The upper and central figures are interpreted, left to right, as representing *H. wortmani*, *H. miticulus*, and *H. powellianus* (possibly as subsp. *browni* in upper figure); and the lower figure only *H. wortmani* and *H. miticulus*.

about the upper limit of the range for *H. miticulus*, as suggested by the composite histogram for the Buffalo Basin materials. Clearly synonymous is Matthew's *H. lysitensis* (pl. 9, fig. 6), originally proposed as a subspecies of *H. mentalis* for the Bighorn Basin Lysite population. Denison's *H. latidens* (pl. 9, fig. 12) for the Indian Meadow materials of the Wind River Basin was based on characters of the lower molars that appear relatively variable.

That a smaller species than the foregoing is present, at least in middle and later Wasatchian time, is clearly indicated in several of the histograms. The oldest name applicable to this is Osborn's *Hyopsodus wortmani* (pl. 9, figs. 7-9), originally described from the Lost Cabin of the Wind River Basin. Its portrayal in the histogram for the Knight beds of the Wasatch in the Green River Basin is even better defined with an observed range there of from 3.4 to 3.9 mm. In the Lysite of the Wind River Basin, representation is more meager but includes the material described by Loomis as *Hyopsodus minor* (pl. 9,

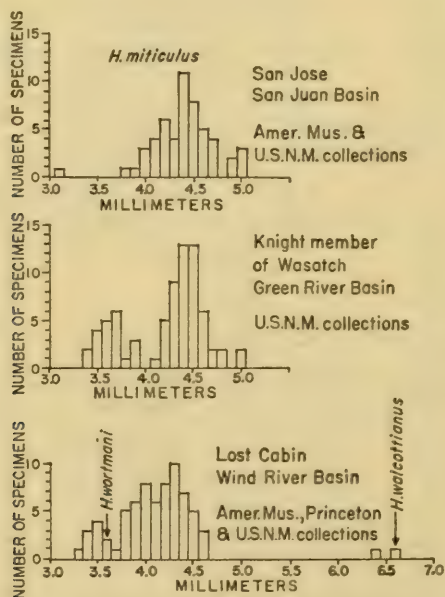


FIG. 5.—Comparison of frequency distributions for length of M_2 in *Hyopsodus* from Lost Cabin horizons in the Wind River and Green River Basins with that for *H. miticulus* of the San Jose beds in the San Juan Basin. Names show positions of specimens that have been described as types. The central figure is interpreted as representing, left to right, *H. wortmani* and *H. miticulus*; and the lower figure, *H. wortmani*, *H. miticulus*, and *H. walcottianus*.

fig. 11). In view of the interpretation made regarding the continuity of *H. miticulus* through the stages of the early Eocene, I can see no justification for recognizing *H. minor* as distinct. No doubt the best display for the small form in the Lysite is seen in the histogram for the mid-section of the Buffalo Basin sequence (fig. 4), with an observed range of 3.0 to about 3.8 mm. The species is also clearly indicated for the late Wasatchian in the Green River (New Fork), and Huerfano Basins. Moreover, there is evidence in the histograms, though extremely limited, of a similar small form in the Gray Bull and San Jose beds. The small *Hyopsodus loomisi* (pl. 9, fig. 4) of McKenna in the Washakie Basin seems to fall within the range for *H. wortmani* but comes from the base of the Wasatchian section and is structurally more primitive than either this species or *H. miticulus*.

Hyopsodus powellianus (pl. 8, fig. 8) is the second of Cope's names for these Wasatchian Eocene species that can be defended as valid. It is based on materials from the Bighorn Basin, and although the level is not recorded, it is almost certainly from the Lysitean interval there represented. The type falls very near the mean of 5.70 pertaining to the larger species having an observed range of 5.2 to 6.2 mm. represented in the upper part of the Buffalo Basin sequence (see figs. 3 and 4).

With regard to the larger species represented in the Lysite of the Wind River Basin, however, the situation is not so easily resolved, and Matthew may have been justified in regarding the form which Loomis named *Hyopsodus browni* (pl. 8, figs. 4, 5) as a subspecies of *H. powellianus*, midway between the latter and *H. mentalis* (= *H. miticulus*). In the Wind River Lysite display the mean for all the materials above 4.5 mm. is 5.23 mm., much less than 5.70 cited above for the Buffalo Basin *H. powellianus*. Moreover, from the histogram it is seen that the observed range of about 4.6 to 5.9 mm. is a little large in comparison with other species, and the frequency distribution looks as though there might have been two species larger than *H. miticulus*; however, the coefficient of variation for this Wind River representation is only 5.5. It is 4.8 for the Buffalo Basin *H. powellianus* material. Synonymizing *H. browni* with *H. powellianus* may be open to question; nevertheless, I seriously doubt the presence of another line of large hyopsodonts in the mid-Wasatchian interval. It seems probable that Matthew's interpretation, that a geographic variant is represented, is the best solution and *H. browni* should not be given full specific recognition. Loomis' *H. jacksoni* (pl. 8, figs. 6, 7)

from the typical Lysite is more easily disposed of, as it is almost identical in size to contemporary *H. powellianus*.

In the Lost Cabin stage of the Wind River Basin remains of a limited number of outstandingly large individuals with a size range widely separated from other Lost Cabin materials, and evidently somewhat beyond the range of Lysitean *H. powellianus*, represent a form Matthew named *Hyopsodus walcottianus* (pl. 8, figs. 1-3). While this may well have been derived from earlier *H. powellianus*, its distinctive size would seem to warrant separate recognition in the latest Wasatchian interval in Wyoming. The form may well be represented also in the late Wasatchian levels in the Plateau Valley and Huerfano Basin in Colorado.

Bridgerian species.—The Bridgerian materials lend themselves particularly well to statistical analysis because of their relative abundance in all levels of the middle Eocene, and so far not complicated by problems of geographic correlation and variation. Moreover, I have included in this study, for statistical purposes, only the relatively large collections in the National Museum because of the more precise information available on stratigraphic positions for the many collecting localities.

The earliest name available for Bridger materials is, of course, that for the type-species *Hyopsodus paulus* (pl. 7, fig. 4). The type-specimen was described by Leidy as having been found by Hayden in the vicinity of Fort Bridger (Church Buttes according to Matthew and Smiths Fork according to the National Museum type-catalog of 1907). No doubt the specimen is from the Blacks Fork member or lower Bridger ("B" of Matthew). In its length of M_2 the type falls essentially at the mode and close to the mean of 4.21 mm. determined for the Grizzly Buttes materials shown in the lower histogram of figure 6. The evidence is rather striking that but a single species is represented in the Grizzly Buttes area, and the coefficient of variation determined for this frequency distribution has a comparatively low value of 4.3. A very similar display is shown for collections obtained from the lower Bridger beds on the east side of the basin (see middle histogram of fig. 6), localities for the most part very high in "B" to the north of Cedar Mountain and around the lower part of Twin Buttes, not far beneath the Sage Creek White Layer which separates the Blacks Fork and Twin Buttes members. In the northerly part of the basin, however, along the Bridger escarpment of middle and lower "B" from near "Millersville" at the confluence of Blacks Fork and Smiths Fork northward to the vicinity of Church Buttes and east-

ward toward Little America, the collections reveal a frequency distribution shown in the upper part of figure 6. The coefficient of variation for this display is about 11.2, demonstrating beyond doubt the inclusion of a second and smaller species accompanying *H. paulus*. The appropriate name for this form is Leidy's *H. minusculus*. Cope's name, *H. vicarius* (pl. 7, figs. 5, 6), would have had priority, but in selecting a type from between Cope's two cotypes Osborn picked the

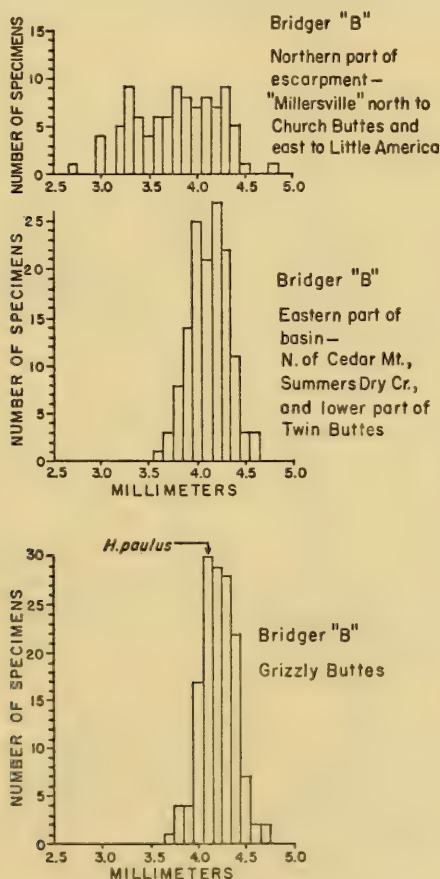


FIG. 6.—Comparison of frequency distributions for length of M_2 in *Hyopsodus* in collections from the southwestern (Grizzly Buttes), eastern, and northerly portion of the lower (B) or Blacks Fork member of the Bridger formation. The upper figure is interpreted as representing a mixture of *H. minusculus* and *H. paulus*. The middle and lower figures represent only the genotypic species *H. paulus*.

larger specimen which falls more clearly within the lower part of the range for *H. paulus*. A composite histogram for all of the *Hyopsodus* material from the Blacks Fork member is shown in the lower part of figure 8. For the figure on the left side showing the frequency distribution for the length of M_2 , a coefficient of variation of only 7.8 is calculated, considerably less than above where the two species are more equally represented. The display in the right lower part of figure 8 shows the position of the type of *H. minusculus* which was described from an upper dentition. Its measurement, however, does not form a

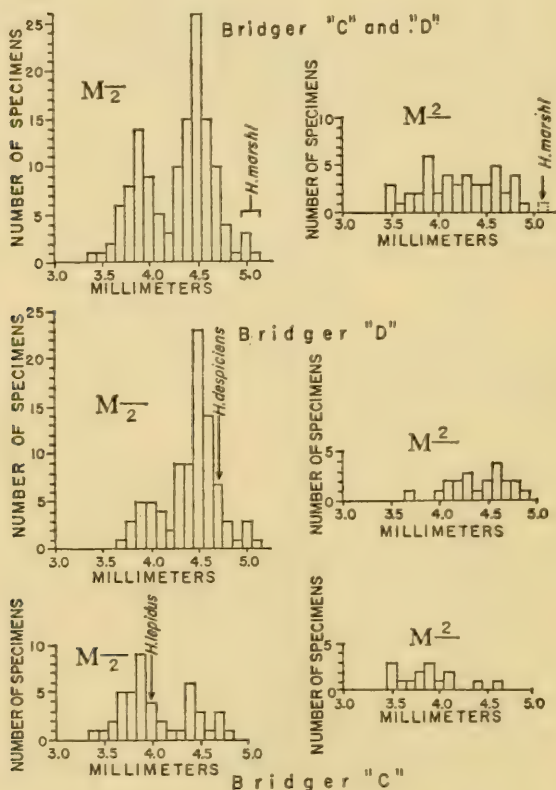


FIG. 7.—Comparison of the frequency distributions for length of M_2 (left) and M^2 (right) in *Hyopsodus* from Bridger "C" and "D," and their composite for the upper or Twin Buttes member of the Bridger formation. Names show positions of specimens that have been designated as types. All six figures are interpreted as representing, left to right, *H. lepidus* and *H. despicens*, with the addition of *H. marshi* in the top two figures.

part of the histogram as the type-specimen is not a part of the collection displayed.

At an occurrence known as the Powder Wash locality in the Uinta Basin, Dr. J. LeRoy Kay obtained a considerable number of small mammal remains from a sandstone lense in the Green River formation. Included was a good representation of *Hyopsodus*. A frequency distribution for length of M_2 very strongly suggests that the form represented is *H. minusculus*. A few upper teeth noted in this collection seem rather large for this species so that possibly *H. paulus* is also included.

In the upper or Twin Buttes member of the Bridger formation two zones are represented, "C" and "D." Frequency distributions for the lengths of both M_2 and M^2 are shown (fig. 7), and those for the lower teeth rather clearly indicate a continuity of the species represented from one zone to the other with very little shift in the means but with a considerable shift in the relative abundance of the forms. The smaller form is more abundant in horizon "C" as represented principally in the Sage Creek basin and in general to the north of Lone Tree, whereas the larger species becomes relatively more abundant in horizon "D" of the same general area, but including also some materials from the Twin Buttes White Layer and above. The means for these two species, determined from the total of materials used for the histogram displayed for M_2 in the upper part of figure 8 are 3.87 and 4.54 mm. with both the mean and mode for *H. paulus* below at 4.2, precisely the nadir point between the modes of the upper graph. It is interesting to note that the shift in means between the lower and upper Bridger is rather abrupt, evidently taking place at the Sage Creek White Layer, although *H. minusculus* is recorded only from the lower levels of the Blacks Fork member. The larger form in "C," moreover, is rather sparsely represented in comparison with the relative abundance of *H. paulus* below. The widespread lacustrial unit separating the two members evidently represents an interval of faunal readjustment and I am inclined, because of the abruptness of the change in situ, certainly so far as *H. paulus* is concerned, to regard the species of *Hyopsodus* represented above as different from those below. Applicable names here would be Matthew's *H. lepidus* (pl. 7, fig. 3) for the smaller species and *H. despiciens* (pl. 7, figs. 1, 2) for the larger. Although Osborn's species name *Hyopsodus marshi* has priority over *H. despiciens* and would appear on the basis of size to be questionably separable, I am tentatively retaining the distinction because of the progressiveness of the upper premolars in the type of

H. marshi. None of the *H. despiciens* from the "D" horizon show, for example, the characters of P^2 described by Matthew.

In a small outlier of Bridger beds in Moffat County, Colorado, a locality known as the Sand Wash Basin, Dr. Mary Dawson obtained

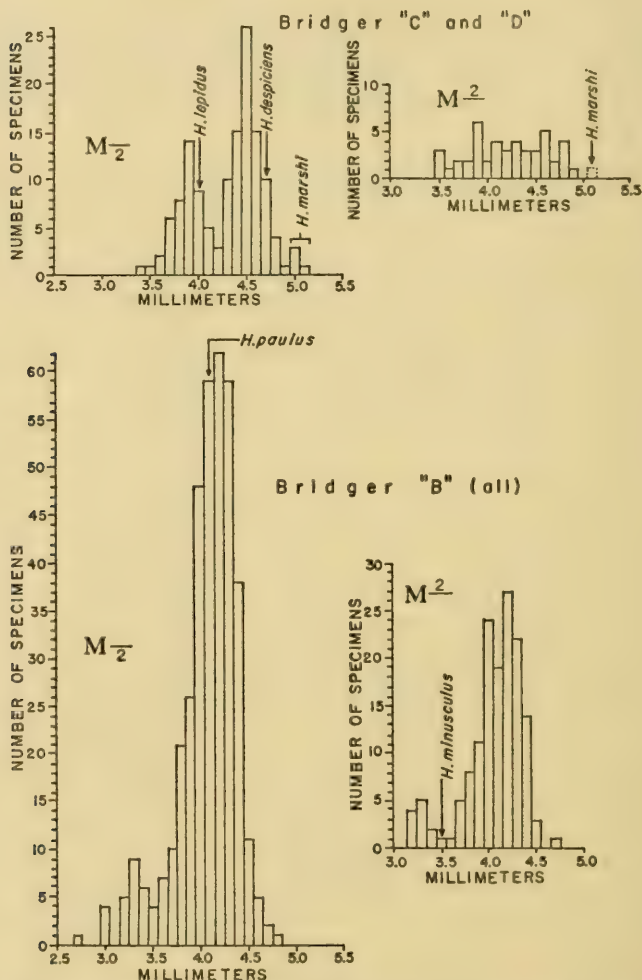


FIG. 8.—Comparisons of frequency distributions for length of M_2 (left) and M_2 (right) in *Hyopsodus* in a composite of materials from localities in the lower Bridger or Blacks Fork member with a composite of materials from the upper Bridger or Twin Buttes member. Names show positions of specimens that have been described as types. The top figures represent, left to right, *H. lepidus*, *H. despiciens*, and *H. marshi*; the lower figures, *H. minusculus* and *H. paulus*.

a collection of *Hyopsodus* materials which shows a frequency distribution for length of M_2 which corresponds very well with that figured for *H. despiciens*. The area is not geographically remote and the above strongly suggests representation of the Twin Buttes member or upper Bridger. This is the same locality from which the Denver Museum of Natural History obtained material described by Abel and Cook as *Hyopsodus markmani* (pl. 9, figs. 13, 14). The latter is regarded as a synonym of *H. despiciens*, as its size is entirely consistent with this disposition. The small M^1 thought to characterize *H. markmani* is a Dp^4 .

A locality known as Tabernacle Butte, within the Bridger Basin, but separated by faulting from the main body of the Bridger formation is purported to be upper Bridger (McGrew, 1959) and the *Hyopsodus* materials identified as *H. lepidus*. This collection was not included in the present study.

Uintan species.—Although material of *Hyopsodus* from the upper Eocene is relatively scarce, the two species that have been named, *H. uintensis* and *H. fastigatus*, both appear to be valid. *H. uintensis* (pl. 9, fig. 2) was described by Osborn on a maxilla from the upper or "C" level of the Uinta formation in the Uinta Basin of Utah, and he referred to it two lower jaw fragments in the American Museum collections. Although the type would appear from the size of M^2 to be a little large (4.3×6.2 mm.), five lower jaws in collections at Yale, Museum of Comparative Zoology, and U. S. National Museum show an observed range of 3.8 to 4.1 mm. for the length of M_2 . This is comparable to the better known upper Bridger materials of *H. lepidus*. It should be noted, however, that the USNM and MCZ specimens are from the White River pocket and hence represent Uinta "B." The levels for the specimens from the Marsh collection are not known, as the information that accompanies them includes only "White River, Utah." Possibly they are also from the lower horizon and Uinta "B" material represents a smaller variant than the type. A maxilla from the White River pocket in the Carnegie Museum collections is of a size comparable to these lower jaws, distinctly smaller (M^2 is 3.85×5.2 mm.) than the type.

Hyopsodus uintensis was tentatively recognized in the upper Eocene Badwater fauna of the Wind River Basin on the basis of an upper molar (Gazin, 1956b). Considerably more material has been collected by Carnegie Museum parties under Drs. Craig Black and Mary Dawson. The combined collections include about 10 recognizable M^2 's showing an observed range in length of from 4.1 to 5.0 mm. The

type of *H. uintensis* (4.3 mm.) falls within the lower part of this. Eleven M_2 's in the Carnegie Museum collection show an observed range of 4.3 to 4.9 mm., a little beyond that for the range thought to represent Uinta "B" specimens. The Badwater teeth show progressiveness characteristic also of the larger *H. fastigatus* material, and an incipient tendency toward the formation of transverse lophs in the upper molars is seen in the figured Badwater tooth (Gazin, 1956b, pl. 1, fig. 3) in which there is a distinctly deeper valley separation between the protocone and hypocone, and these cusps are more strongly united with the accessory cuspule anterolateral to each than they are to each other. M^2 in the type of *H. uintensis* likewise shows this tendency (see pl. 9, fig. 2). Moreover, the crescentic crests of the lower molars, together with the anterior and posterior walls of these teeth, are decidedly more oblique than in Bridger material.

The relatively large upper Eocene form described as *Hyopsodus fastigatus* (pl. 9, fig. 3) by Russell was based on some isolated teeth from the Swift Current Creek beds in Saskatchewan. Its size, as indicated by the type lower molar, is rather close to that of *H. marshi* in the upper Bridger; however, while the *H. marshi* type exhibits progressive premolars, *H. fastigatus* is more advanced in a tendency toward more lophodont upper molars and more obliquely crescentic lower molars, as noted in referred materials and the Badwater *H. uintensis* material mentioned above. Quite the best material believed to represent *H. fastigatus* has been found at an upper Eocene locality discovered by G. D. Robinson near Shoddy Springs, approximately 8 miles to the northwest of Three Forks, Montana. The beds here have been called the Climbing Arrow formation by Robinson, but are, no doubt, the Thompson Creek beds of Douglass, at a lower horizon, however, than that which produced Douglass' Chadronian material. Two maxillae in the Carnegie Museum collection and one in the USNM show a range in length of M^2 of from 5.1 to 5.3 mm., about the size of earlier *H. marshi*, as noted above. A lower jaw in the Carnegie Museum collection exhibits an M_2 with the dimensions 5.2×4.2 mm., about the same length but slightly broader than observed in a cast of the type of *H. fastigatus*, regarded by L. S. Russell as M_2 . Lower molars in the Montana jaw show the rather prominent development of the metastylid noted by Russell. This cuspule is usually present in the earlier materials, but is somewhat less conspicuous. Moreover, the hypoconulid on the anterior molars is close to the entoconid and together they form with the parastylid of the succeeding tooth a better crest than in earlier forms.

ENVIRONMENT

Unlike *Meniscotherium*, *Hyopsodus* appears to have been present in essentially all local mammalian faunal assemblages within the Eocene of the Rocky Mountain Region. For this reason the genus has much less significance as an indicator of any particular habitat. In consequence we are faced with the entire range of environments suggested by the biota and characteristics of the enclosing sediments for the various basins throughout the Eocene. These will, of course, denote the surroundings in which these animals lived, whereas their particular adaptation or habits are to be interpreted from details of morphology, and this in turn by analogy in comparison with living forms.

Considering first details of distribution for particular species, a somewhat anomalous situation was noted (Gazin, 1965, p. 17) in the earlier Eocene with regard to the larger species, *H. powellianus* and *H. walcottianus*, in which it seemed that these, but not the smaller species, may have been incompatible with *Meniscotherium*. A further peculiarity was noted in plotting frequency distributions in tooth sizes. Where one of these larger species is represented in an assemblage there is a definite shift in the mean to a lower figure for the smaller species in comparisons made between materials from beds of nearly the same age, such as between the upper Knight of the Green River Basin and the Lost Cabin of the Wind River Basin (fig. 5), or as between succeeding zones of Lysite age in the Buffalo Basin (fig. 4). Assuming that the pattern of species identification is correct, it would appear as though a factor of incompatibility was here involved between individuals of different species too near the same size, where *H. powellianus* or *H. walcottianus* were concerned. Nevertheless, the downward shift in range and mean for the smaller forms is actually rather small.

With regard to the more general features of the earlier Eocene or Wasatchian time, I (1965) have previously considered the pertinent evidence for conditions as they related to the occurrence or absence of *Meniscotherium*. The conditions prevailing would appear to be resolved into a predominantly savannah-like environment on the one hand, and a much more paludal or swampy situation on the other, but with no dearth of trees in either as implied by the occurrence and variety of primates, and in both of which *Hyopsodus* was common. Likewise a somewhat open terrain seems evident from the perisodactyls, with *Hyracotherium*—ungulate, of course, though not so

decidedly cursorial as later—as universal in occurrence as *Hyopsodus* and actually exceeding it in numbers at many localities.

The advent of the extensive lake system in which the Green River deposits were laid down no doubt altered the environment considerably. The origin of the lakes was tied to orogenic activity, and in southwestern Wyoming their development began in later Wasatchian time. This seems, however, to have had no effect on the abundant representation of *Hyopsodus*, although in areas in which the lake advanced and retreated there would appear to have been some change in the relative abundance of the different species, as from below to

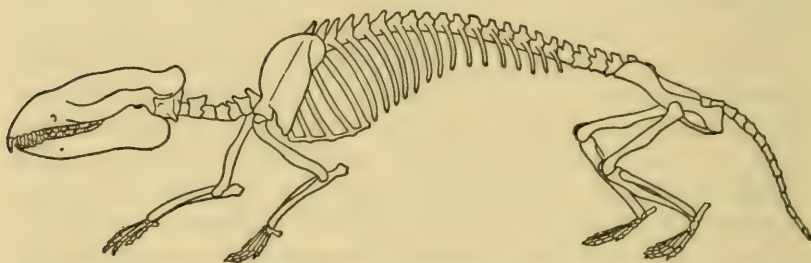


FIG. 9.—*Hyopsodus paulus* Leidy. Drawing based for the most part on associated skeletal material (caudal vertebrae conjectural) of USNM 23740, and in part on USNM 17980, from the lower Bridger beds of southwestern Wyoming. Approximately one-third natural size.

above the Tipton or Fontenelle tongue in the upper Green River Basin, or an actual redistribution of species, as from below to above the Sage Creek White Layer in the Bridger sequence.

The Green River formation itself has yielded the materials which have been most pertinent to a better understanding of the physical and floristic environment of much of Eocene time. The work of others, particularly the limnological studies of Dr. Wilmot H. Bradley and the paleobotanical reports of Dr. Roland W. Brown, both of the U. S. Geological Survey, have been most enlightening. These have been previously cited (in Gazin 1965 for the earlier Eocene and 1958 for the middle and later Eocene) and summarized. The studies included demonstration of a warm temperate climate with a plentiful rainfall, low basin altitude, and high relief for the surrounding mountains. During the middle Eocene time, moreover, when *Hyopsodus* achieved faunal supremacy in numbers of individuals there is evidence of considerable volcanic activity in the form of ash falls with much reworked ash throughout the fluvial and lacustrine sequence.

It is not until upper Eocene time that this supremacy in numbers is lost, a time of increasing aridity as noted by Bradley (1936), but the mammalian evidence for this is seen in the increasing hypsodonty of associated ungulates, and almost explosive distribution of grazing type artiodactyls. This was further accompanied by near extinction or retreat of the primates, so well represented in the middle Eocene, no doubt in a large measure resulting from floristic changes. During upper Eocene time, moreover, a selective effect is evident in the incipient trend toward a more lophodont and more hypsodont dentition in *Hyopsodus*, as noted in a foregoing section, presumably in

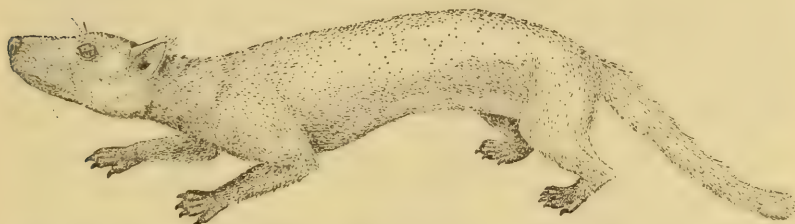


FIG. 10.—Restoration of *Hyopsodus* by Lawrence B. Isham, based on skeletal drawing (fig. 9).

response to increasing aridity and coarser food. Perhaps foretelling extinction, at least so far as the record is known, is the striking increase in the relative number of immature specimens encountered in upper Eocene sediments, which are exceedingly rare in the early and middle Eocene occurrences, except for a single nest of juvenile specimens of *H. lepidus* encountered by Granger and Matthew in the upper Bridger. I strongly suspect that, although *Hyopsodus* was apparently so adaptable to the range of conditions prevailing in the early and middle Eocene, the more drastic change in climate, and inevitably the vegetation, during upper Eocene time eventually proved too great for its particular adaptations. The possibility of more efficient predators, however, cannot be ruled out.

With regard to the adaptive specializations, certain details of which are noted in the following sections, *Hyopsodus* is seen as a somewhat elongate, perhaps weasel-like, animal (figs. 9 and 10) approaching the hyrax in the number of dorsal vertebrae. The limbs seem relatively short, particularly the lower part of the limb with respect to the upper. The somewhat elongate rostrum and nearly *Erinaceus*-like anterior incisors suggest a rooting habit. This is further emphasized by indications of neck and shoulder musculature involved in such a

habit. Features of the fore limb and scapula, moreover, strongly suggest a digging habit as well, possibly in grubbing for food. The pelvis and hind limbs show marked leverage for muscles pertinent to both flexion and extension, but perhaps more noticeable are evidences for importance of those which might be used in jumping when alerted. The shortness of the limbs, relative to body size, would not, however, suggest extended running or leaping, such as characterizes the longer legged lagomorphs. Articulations in the limbs and feet, moreover, would permit considerable flexibility or diversity of movement.

One may further speculate from the prominence of the corpora quadrigemina of the exposed midbrain, as revealed in the endocranial cast, that sight and hearing were relatively acute, particularly the latter. Possibly, however, these were not too highly organized, inasmuch as the neocortex seems somewhat restricted. Matthew (1928) was inclined to regard *Hyopsodus* as semiarboreal.

THE SKELETON OF HYOPSODUS

SKULL

The skull of *Hyopsodus* in overall appearance is comparatively slender and elongate, rather more so than the much larger skulls of the condylarths *Phenacodus* and *Meniscotherium*. In size the skull of *Hyopsodus paulus* is rather close to that of the hedgehog *Erinaceus europaeus* and there is a resemblance between these in the general form of the rostrum. The anterior incisor is enlarged (pl. 6, fig. 1), but somewhat less so than in *Erinaceus*, and the length of the tooth row is about half the length of the skull. Both lack postorbital processes, but *Hyopsodus* is much narrower across the frontals, as it is at the postorbital constriction. The cranial portion appears elongate and slender, somewhat more didelphid-like than erinaceid, and like the opossum, has much deeper zygomatic arches (pl. 11, fig. 1). The temporal fossae, however, are more deeply excavated and the lambdoidal crest is more protruding than in *Didelphis*, while the sagittal crest, more as in *Erinaceus*, is not nearly so well developed. Certain details of the *Hyopsodus* skull were earlier (Gazin, 1965) discussed in a comparison with *Meniscotherium* and *Phenacodus*. A part of this is repeated and expanded.

Dorsal view.—In dorsal view the rostrum tapers forward noticeably from the anterior margin of the orbital rim to the anterior narial aperture. The nasals extend forward to this aperture, about as in *Erinaceus*, but are much more broadly exposed than in that form. They are relatively narrower and do not project so far forward as in

Meniscotherium. Posteriorly they terminate abruptly just back of the frontomaxillary suture (pl. 2, fig. 2), not penetrating the frontal area so deeply as in *Meniscotherium*. They broaden slightly at the narial aperture but their greatest width appears to be at the frontomaxillary suture.

Unlike *Erinaceus*, the dorsal surface of the skull tapers backward sharply from the greatest rostral width, at about the anterior margin of the orbits, to the postorbital constriction which is decidedly narrow across the roots of the olfactory lobes of the brain. The frontals are narrow and gently convex transversely over the dorsal surface, making limited contact with the maxillae forward between the nasals and lacrymals, the latter being noticeably expanded forward and medially from the orbital rim. The weak temporal crests, in the absence of postorbital processes, converge posteriorly from the orbital rim with little or no flexure to form the low sagittal crest, which commences at about the postorbital constriction. This is also at about the point where the frontoparietal suture crosses the midline of the skull.

The cranial portion of the skull broadens more gradually posteriorward, toward its greatest width across the squamosal roots of the zygomatic arches. The arches are moderately expanded and join the cranium well forward of the lower extremities of the lambdoidal crest. With the prominent and elongate upturn of the occipital crest, there is produced a broad, more distinct dorsal concavity, just over the midbrain, in the posterior portion of each of the temporal fossae, than, for example, in the hedgehog. The depths of these fossae are penetrated by a somewhat irregular cluster of vascular foramina near and at the parietosquamosal suture. The parietosquamosal suture runs forward from the suture bounding the supraoccipital, from a point about half way down the lambdoidal crest and a little above the upper limit of the mastoid exposure on the occiput. The suture divides the temporal fossae posteriorly about equally between the parietal and squamosal but then descends rapidly on the lateral wall of the braincase just anterior to the zygomatic roots. The posteriorward flare of the lambdoidal crest is somewhat greater on either side of the posterior extremity of the sagittal crest, somewhat as in *Meniscotherium*. There is no evidence for an interparietal.

Lateral view.—In lateral view the premaxilla is broadly developed ventrally along the alveoli for the incisors (see pl. 6, fig. 1) and tapers upward and backward, wedging out posteriorly between the maxilla and nasal at a point at least half way along the length of the nasal. In this view also the relatively greater length of the first incisor is evident, approaching the development in *Erinaceus*. The lateral

exposure of the maxilla is relatively elongate to accommodate the long cheek tooth series, and moderately deep posteriorly. The infra-orbital foramen is large, well forward, and close to the tooth row. Its position is just above the posteroexternal root of P^3 . The vertical development of the jugal is relatively great and its upper margin joins the lachrymal forward, eliminating the maxilla from participating in the orbital rim, not at all like *Erinaceus*. A process of the maxilla, however, extends posteriorly for an appreciable distance along the inner surface and lower margin of the arch (see pl. 4, fig. 1). The lachrymal, forming a part of the anterosuperior margin of the orbit, extends a short distance forward to the maxilla and upward or medially to the frontal. The large lachrymal foramen is concealed behind the orbital rim, quite unlike *Erinaceus*. The considerable depth of the zygomatic arch is maintained throughout its length (pl. 11, fig. 1), posteriorly to a position just above the postglenoid process. The superior margin from there descends above the external auditory meatus, forming the lateral margin of the cranium to the ventral extremity of the lambdoidal crest at the root of the mastoid process. The jugal portion of the arch extends posteriorly beneath the squamosal almost but not quite to the glenoid surface. Superiorly the zygomatic process of the squamosal extends forward about half the length of the arch.

Within the orbital fossa, the orbital plate of the maxilla appears as a roughly triangular area, and near its medial margin can be seen the irregular trace of the maxillopalatine suture. The suture extends from just lateral to the small posteromedial notch well forward toward the relatively large posterior aperture of the infraorbital foramen. Medial to this suture, and to the posterior margin of the orbital plate of the maxilla, the sphenopalatine foramen, as I have noted earlier (Gazin, 1965, p. 26), is about even with or slightly posterior to the hind margin of the last molar. The optic foramen is well in advance of and a little higher than the sphenoidal fissure. Its position is just ahead of the anteroventral margin of the surface for the temporal muscle, and directly below the postorbital constriction. There is evidently no alisphenoid canal, although this was earlier (loc. cit.) thought possible, nor is there any certain indication that the foramen rotundum is partitioned from the sphenoidal fissure. The latter appears as a somewhat elongate (anterodorsal-posteroventrally) opening which, in turn, is situated in a deeply pocketed area well back and beneath the crest bounding the inferior margin of the temporal fossa.

Occipital view.—In the occipital view of the *Hyopsodus* skull the lambdoidal crest is seen, in rare instances where sufficiently well pre-

served (pl. 4, fig. 3; pl. 5, fig. 2, the crest here is supported by a fringe of matrix on its posterior surface), to be high and generally upward flaring, although slightly posteriorward on either side of the mid-section. The crest is decidedly thin and but weakly buttressed by upward diverging crests on the occipital surface. Its development, though, appears rather unusual in so small a mammal, much more impressive than in *Erinaceus*, suggesting good leverage for the splenius and other muscles of the neck. If the trapezius is included this may correlate with the remarkable development of the spine of the scapula. The lower half of the lambdoidal crest is formed on the squamosal; median to this on the occipital surface the mastoid is exposed, but facing obliquely, and broadening downward to occupy the space between the paroccipital process and the mastoid process which it forms at the lower extremity of the lambdoidal crest. The paroccipital process is conical and close to the occipital condyles, evidently not nearly so elongate as in *Meniscotherium*.

Palatal view.—The *Hyopsodus* palate is relatively elongate between a full complement of cheek teeth, and the lingual margins of the tooth rows are nearly parallel, or slightly converging anteriorly. The anterior margin of the palate, or premaxillary portion, is evenly rounded lingual to the incisors, and the two lateral incisors have a more longitudinal than transverse alignment posterolateral to the larger first incisor. The anterior palatine foramina, though small, are conspicuous and relatively elongate posterolaterally, extending from near the first incisor to about a line between the third incisors. Except for a small segment of the posterior margin of each they are essentially surrounded by the premaxillae. The premaxillo-maxillary suture extends anteromedially from the canine alveolus to the posterior tip of the anterior palatine foramen, then continues posteromedially for a short distance to the median suture. Small nutrient foramina in the palate are noted irregularly scattered between the premolars.

The palatines are broadly exposed posteriorly and the maxillo-palatine sutures on each side extend forward from the posterior margin of the palate to the lingual margin of the alveolus for the inner root of M^3 . Continuing forward close to M^2 the sutures then converge to the midline of the palate at a point about even with the anterior margin of M^1 . Posterior palatine foramina are small and relatively inconspicuous but are seen to occur at or near the maxillo-palatine suture. The anterior margin of the posterior nasal aperture shows an everted, liplike rim or crest, evidently for the tendon of the tensor palati, better developed than in *Meniscotherium* or *Phenacodus*, but not so prominent as in *Erinaceus* or *Didelphis*. This margin, how-

ever, is more transverse and does not extend so far forward in the palate as in *Meniscotherium*. It is about even with the posterior margin of the third molar. Moreover, the maxillary tuberosity is close to the lateral margin of the narial aperture so that there is only a very small notch between them in contrast with the deep and broadly open saddle noted in *Meniscotherium*.

Basicranium.—The basicranium in *Hyopsodus* (pl. 1; pl. 3; and pl. 4, fig. 1), as in *Meniscotherium*, is relatively elongate. This is noticeable in the forward position of the glenoid surfaces with respect to the occipital condyles and the length of the mesopterygoid fossa. The basicranium is decidedly unlike that in *Erinaceus*. The elongate basisphenoid and basioccipital area is gently concave in the mesopterygoid fossa and moderately convex posteriorly with its greatest width close to the foramen magnum. An elongate ventral protuberance, contributing to the posterior convexity on the basisphenoid and basioccipital, reaches apices on both sides at about the suture between these bones (pl. 3). These may be further emphasized by a transverse crest at the suture (pl. 1; pl. 4, fig. 1). This condition evidently testifies to the significance of the rectus capitis anticus major that functions in depressing the snout. As in *Phenacodus*, this seems more important than in *Meniscotherium*. The pterygoid fossa is well developed, possibly more so than in *Meniscotherium*, relative to size, but not so broad and deeply excavated as in *Erinaceus*. More recently prepared material (since Gazin, 1965) shows that the pterygoid proper, though somewhat less elongate anteroposteriorly than the pterygoid plate of the alisphenoid, projects downward more than the latter (not less developed as stated in 1965), although this portion is not sufficiently well preserved to exhibit the character of the hamular process. The posterior margin of the pterygoid plate of the alisphenoid ascends steeply to a point near or immediately in front of the foramen ovale. There is no evidence of an alisphenoid canal, such as in *Meniscotherium*, so that apparently the external carotid (internal maxillary) artery remained outside the cranial wall or alisphenoid, although, of course, some portion of the carotid system, such as one of the meningeals, may well have occupied the foramen ovale, as well as the inferior maxillary or mandibular nerve (V_3).

There is a strong crest posterolateral to the foramen ovale, as in *Meniscotherium*, the styloid process of Cope, made up of plates from the alisphenoid and squamosal, but with somewhat greater participation of the squamosal than the alisphenoid, and is much closer to the glenoid surface and postglenoid process leaving a relatively wider separation between the crest and the foramen lacerum medium in

Hyopsodus. The position of the crest is near or about that of the angular spine of the alisphenoid in man, which supports a portion of the musculature of the soft palate and of the tympanum. Possibly its prominence is to be correlated with the conspicuous lip-like rim at the posterior margin of the palate for the tensor palati. Nevertheless, as stated earlier (Gazin, 1965), I suspect that here it may be homologous to a similar prominence in certain other mammals, such as the oreodonts, where it forms a pedicle for the support of the anterior portion of the bulla. As in the case of *Meniscotherium*, however, no bulla has been discovered for *Hyopsodus*. Its position also recalls somewhat the alisphenoid bulla in didelphids but is differently oriented and very much less developed. A broad groove in the alisphenoid for the eustachian tube, close to the foramen lacerum medium is better separated from the crest or pedicle, attributed to a possible bulla, than in *Meniscotherium*.

The glenoid surface for articulation of the lower jaw in *Hyopsodus* is transversely elongate and only slightly concave in this direction, rather different in this respect from the more obliquely elongate and deeply concave surface in *Meniscotherium*. The postglenoid process, posterior to the inner half of the glenoid surface, is well developed, and posterointernal to it the large postglenoid foramen has its aperture completely surrounded by the squamosal. The broad arch of the squamosal over the external auditory meatus extends posteriorly down the anterior surface of the moderately developed mastoid process which is anterolaterally well separated from the paroccipital process, leaving the mastoid better exposed ventrally than in *Meniscotherium*. A deep groove in the mastoid, extending dorsoventrally just median to the mastoid process, is the stylomastoid foramen for the facial nerve, but in the absence of a bulla does not appear to be closed anteroventrally. The paroccipital process is a prominent conical form, directed slightly backward but not nearly so elongate nor flattened as in *Meniscotherium*. The condylar or hypoglossal foramen is located decidedly medial to the paroccipital process, close to and partially concealed by the anteroventral margin of the condyle. The foramen lacerum posterius is a rounded, slightly elongate aperture immediately anteromedial to the paroccipital process and seeming to penetrate its root. It is bounded forward by the posterior margin of the petrosal very near the fenestra rotunda.

Periotic.—The petrosal in *Hyopsodus* appears long and slender in ventral view, as a slender cone with its apex directed forward and medially. The promontorium is not separately defined. The relatively large fenestra rotunda faces backward, outward, and downward. Its

posterior rim is joined by a crest from the medial portion of the ventrally exposed mastoid, which also forms an anterior root or buttress for the paroccipital process. This crest at the posterior rim of the fenestra rotunda may also have supported a stylohyal. Just medial to it is the comparatively large foramen lacerum posterius, and laterally the groove for the facial nerve. The relations here are closely similar to those in *Meniscotherium*. Anterodorsal to the fenestra rotunda is the smaller, outward facing fenestra ovalis. As in *Meniscotherium* the facial nerve would emerge from an aperture anterodorsal to the fenestra ovalis, descend to a position opposite the fenestra ovalis, turn backward then downward to appear anterolateral to the root of the paroccipital process, were the area covered by a bulla.

The medial margin of the petrosal in *Hyopsodus* shows a broad longitudinal groove partially formed by the lateral margin of the basioccipital. The posterior extremity is determined by the point at which the petrosal more solidly abuts the basioccipital, close to the foramen lacerum posterius. This groove clearly opens into the cranial cavity medial to the anterior extremity of the petrosal where it abuts the alisphenoid. It no doubt carried the internal carotid artery, as interpreted for *Meniscotherium*.

The dorsomedial surface of the petrosal is partially preserved in two specimens for which incomplete and somewhat distorted endocranial casts are illustrated (pl. 5, fig. 1; and pl. 6, fig. 2). The details of this surface of the petrosal are discussed on pp. 42 and 43.

ENDOCRANIAL CAST

It has been possible to prepare partial endocranial casts in latex from two specimens of *Hyopsodus*. One of these (pl. 5, fig. 1) was obtained from assembled cranial fragments (pl. 5, fig. 2) of a specimen of *Hyopsodus miticulus* found in the Knight beds of the Wasatch north of Big Piney, Wyoming. Its identity is based on an included rostral portion with most of the cheek teeth. The other (pl. 6, fig. 2) was prepared from a skull of *H. paulus* in which the base of the endocranium was exposed in a rock surface through weathering. This specimen, including a nearly perfect palate (pl. 6, fig. 1), was found in the lower part of the Bridger formation about 10 miles east of Lyman, Wyoming. In a third specimen (*H. miticulus*), a weathered rostrum only (pl. 2, fig. 1), a natural cast of the olfactory lobes is preserved, together with bone traces showing the position of the cribiform plate and the configuration of the turbinates. Also shown are the rather deep roots of the nasals, normally concealed by the maxillae.

The *H. miticulus* endocranial cast (pl. 5, fig. 1) is not complete anteriorly, nor is the basal part included. Nevertheless, the dorsal surface of the midbrain segment and much of the cerebellar representation is preserved, also configuration of the surface adjacent to the petrosal and the greater part of the surface of the medulla oblongata. In the dorsal view it is seen that the posterior limit of the neopallium is widely separated from the lobes of the cerebellum, leaving the tectum of the midbrain broadly exposed.⁶ The most significant feature here is clear delineation of the corpora quadrigemina. The posterior pair of culiculi, for auditory stimuli, are appreciably larger than the anterior or visual culiculi. There is an appreciable exposure of the midbrain in *Meniscotherium* but the quadrigemina are not evident, possibly because the tectum is rather obscured by the large lateral sinuses. The longitudinal sinus in the *Hyopsodus* cast is evident between the medial margins of the neopallium, and the transverse or lateral sinuses separate just ahead of the anterior culiculi and extend obliquely backward and downward, paralleling the occipital lobes of the cerebral mantle. It is interesting to note that, at the point of separation, the left lateral sinus is slightly higher than the right, recalling the same situation, but more pronounced, in *Meniscotherium*.

The vermis of the cerebellum is relatively large and elevated about to the extent of the cerebrum. The lateral lobes are moderately developed and set off from the vermis by a broadly shallow paramedian fissure. The width across the cerebellum, however, is comparatively constricted, in part as a result of lateral compression of the cranial portion from which the cast was made. Beneath the lateral lobes of the cerebellum there may be seen in side view prominent representation of the superior petrosal sinus, continuation of a part of the transverse or lateral sinus system. On the dorsoposterior margin of this there is evidence of a small foramen indicating vascular communication with the occiput at or close to the dorsomedial margin of the mastoid. Ventrally the sinus curves slightly forward beneath the inner margin of the petrosal to the foramen lacerum posterius. Just posterior to this flexure, on the side of the medulla oblongata, there is a noticeable protuberance representing the form of the hypoglossal or condylar foramen. A subdued ridge between

⁶ Edinger (1964) did not regard the midbrain exposure in mammals as necessarily primitive, but of secondary development. It should be noted, however, that the early forms on which this judgment was based, the multituberculates and *Triconodon*, with an essentially concealed tectum, are not eutherian, nor are they in the line or lines of descent of such mammals, and may even have been independently derived from the therapsids.

this prominence and the sinus is evidently representation of a small vascular structure participating with the hypoglossal nerve in use of the condylar foramen. In the area covered by the petrosal a prominently developed flocculus, nearly globular in shape, projects outward, downward, and somewhat backward. Ventromedial to this the prominence representing the internal auditory meatus, though less projecting, is of a little greater diameter. A division at its apex into the foramen for the facial nerve forward and above, and the auditory nerve posteroventrally, is only faintly discernible on the cast, but clearly evident on the bone. It should be noted in this lateral view of the cast that indication for the depth of the foramen magnum is distinctly exaggerated (pl. 4, compare fig. 3 with fig. 2).

The cerebral portion of the *H. miticulus* cast is not complete and it would appear that a considerable portion of the forebrain is not represented in any of the material at hand. The rostral portion mentioned (pl. 2, fig. 1) of another specimen, however, shows the configuration of the olfactory lobes as seen from above. These are clearly of relatively large size. Their combined diameter is only a little less than that across the lateral lobes of the cerebellum in the specimen figured in plate 5.

The cast of the basal part of the endocranium, taken from the specimen of *Hyopsodus paulus* (pl. 6, fig. 2) shows interesting detail, but to a rather limited extent, as the more elevated structures of the original specimen were partially obliterated by weathering; only the depressed areas, shown as elevated in the cast, are at all well preserved. The olfactory lobe as seen on the right side is incomplete anteriorly but extends downward, transversely somewhat compressed, or longitudinally crested. This is almost immediately anterior to the position of the optic foramen, also here preserved only on the right side. Weathering, moreover, has obliterated all but the weakest trace of the chiasmatic groove for the optic chiasma, which would have been very close to the roots of the olfactory lobes at the postorbital constriction. Well back of this position, about midway on the cast, is seen the well-rounded, moderately large, dome-like surface of the hypophysis or pituitary body. The original bone surface posterior to the hypophysis was destroyed so that there is no trace or representation in depth on the cast of the dorsum sellae. Posteriorly the medulla oblongata appears broad and elongate. On either side of the hypophysis are seen the decidedly prominent representation of the cavernous sinus, terminating forward at the position of the posterior aperture to the sphenoidal fissure, and comprising a complex of vascular struc-

tures and cranial nerves (III to VI, except V_3). Except for the good depth forward there would appear here no evidence of a separate alisphenoid canal or foramen rotundum, with the contents normal for these emerging into the orbital fossa through the somewhat elongate sphenoidal fissure or foramen lacerum anterius. Well back on the ridge there is indication for an elongate slit-like internal aperture of the foramen ovale for the third branch of the trigeminal nerve. Lateral to the cavernous sinus the cast shows, on the right side only (observer's left), the large and elongate pyriform lobe, not sufficiently complete, however, to show the rhinal fissure, so that between the two casts there is no information on the extent to which the lateral lobes of the neopallium may have enveloped the rhinencephalon. Moreover, in no part is representation of the sylvian fossa preserved. Posterior to the pyriform lobe the cast represents only the damaged dorsomedial surface of the petrosal, although the position of the flocculus and the apex of the contents of the internal auditory meatus can be located, and a trace of the cochlea just anterior to the latter can be recognized. Median to the petrosal position the elongate foramen lacerum medium is prominently portrayed, on the left as well as the right side, and this appears connected by a posteriorly much subdued inferior petrosal sinus to the foramen lacerum posterius. A short distance posterior to this, on the side of the medulla oblongata as exposed, can be seen representation of the contents of the hypoglossal foramen.

MANDIBLE

In lateral view the lower jaw of *Hyopsodus* (see pl. 2, fig. 3; pl. 11, fig. 1; and various plates of type-specimens) is rather variable in the amount of forward taper, and often this is rather slight beneath the cheek teeth, but with an elongate taper through the symphyseal portion. Usually the rami are strongly ankylosed throughout the elongate symphysis. The small but long rooted anterior incisors are decidedly procumbent. The number and position of the mental foramina are rather variable, but generally two or three are seen beneath from about the first or second premolar to the fourth, slightly below the middle of the jaw. On occasion, however, only one or even four have been observed. Moreover, anteriorly two small foramina, one on each side, are present adjacent to the symphysis about midway on its length.

Posteriorly on the jaw the masseteric fossa terminates forward in a slight rugosity beneath about the posterior margin of M_3 . Above this the rather well-defined crest limiting the masseteric fossa anteriorly merges with the steeply rising anterior margin of the ascending

ramus. The coronoid process, extending moderately well above the level of the sigmoid notch, has a convex anterior margin but the posterior margin is evidently more nearly vertical, so that the process does not appear to be directed backward over the sigmoid notch so much as in *Meniscotherium*, and may be relatively a little wider at the base. Also beneath about the posterior margin of M_3 the lower margin of the jaw shows a weak to moderately strong concavity, posterior to which the angle of the jaw may, though not invariably, be directed noticeably downward. While not actually complete in any specimen at hand, the angle appears to be relatively large, but possibly not as backward flaring as in *Meniscotherium*. Nevertheless, the condyle sets well forward of the posterior margin of the angle and has little or no neck. Its articular surface is broad medially and the long axis is directed more transversely than in *Meniscotherium* and is not so strongly convex.

On the medial surface of the lower jaw the mylohyoid crest is clearly discernible from just above the partially divided pit for the digastric muscle to a point nearly beneath M_3 . It is approached by a weak crest extending downward and forward from the anterior margin of the ascending ramus from which arises a part of the superior constrictor in human anatomy. The inferior dental canal opens posteriorly in a moderately elongate aperture a little forward of a point midway between the third molar and the condyle, at a level about even with the alveolar margin of the ramus or a little lower, appreciably lower than the condyle. Below this position the inferior margin of the ramus curves inward slightly, beneath the rather large surface for the pterygoid muscles, which in turn may be correlated with the development of the pterygoid fossa in the basicranium.

DENTITION

Hyopsodus exhibits a full complement of 44 teeth. The incisors, canine, and first premolar above and below are comparatively simple, nearly spike-like, single-rooted teeth. They are somewhat like those in *Meniscotherium*, but a little more conical. Moreover, the first upper incisor is relatively larger and P^1 is evidently never two-rooted, as it appears to be occasionally in the latter form. The nearly *Erinaceus*-like enlargement of the first upper incisor, together with the following simple and smaller, but subequal, anterior teeth has been noted; however, this resemblance does not extend to the uniformly small lower anterior teeth. Possibly, nevertheless, the relatively omnivorous diet of the hedgehog may be indicated for *Hyopsodus*.

The cheek teeth seem a little less bunodont than in *Phenacodus* and with much less tendency toward rugosity, extra cuspules, and styles. They are decidedly less progressive in the achievement of a more hypsodont and crescentic pattern characterizing *Meniscotherium*.

Upper dentition.—The large I^1 with its elongate, curved root, apparently determining the contour of the lateral margin of the narial aperture, has a nearly erect, somewhat elongate and tapering, enamel covered crown, with weak evidence of a cingulum at the medial and posterolateral angles. In cross-section the crown is almost triangular, but with a well-rounded anterior angle and a straight, relatively broad posterior margin. The posterior bevel of this tooth clearly occludes with both the first and second procumbent lower incisors. There is a small diastema between the alveoli of the right and left first incisors, not so great as in *Erinaceus*, and the crowns converge slightly downward.

The smaller I^2 , I^3 , C, and P^1 are very much alike, increasing slightly in size posteriorly to the canine, although the canine crown does not reach the length of I^1 . P^1 is smaller than C, about the size of I^3 , but with a slightly lower crown. These anterior teeth are all acutely conical with a well-rounded anterior to lateral surface. There is a somewhat compressed or crested anteromedial margin, slightly convex in profile; and a similarly crested but more nearly straight or slightly concave posterior margin. The posteromedial surface, unlike I^1 , shows a prominent rib. The cingulum is very weak, except at the upper extremity of the anteromedial and posteromedial crests.

P^2 is a two-rooted tooth, more elongate anteroposteriorly than P^1 , often with a very weak anterior style and a somewhat more distinct posterior style. The cingulum may be developed posterointernally. In the earlier or Wasatchian materials this tooth is relatively narrow transversely, although increasing somewhat in width posteriorly. In the Bridger materials this tooth has become decidedly broader with a triangular outline in occlusal view. It has the appearance of a three-rooted tooth, but almost invariably the very broad posterior root is undivided. Only in the type of *H. marshi* from the upper Bridger have I observed conspicuous development of a lingual cusp or deuterococone.

P^3 is invariably a three-rooted tooth with a prominent, single outer cusp and a narrow lingual talon exhibiting a smaller but usually prominent deuterococone. A crest may be developed from the apex of the deuterococone to an anteroexternal style; posterolingually a cingulum extends from the posterolingual wall of the deuterococone, or its apex, to a posteroexternal style. The external cingulum may be weak

or absent across the outer rib of the primary cusp, but is prominent close to the styles. In the Wasatchian or early Eocene material the outer wall of this tooth is relatively elongate, with generally better developed styles, particularly the anterior, giving this tooth a more decidedly triangular outline in occlusal view. By middle Eocene time, however, this outer wall has become much shorter anteroposteriorly, with the anterior and posterior walls approaching parallelism, and the deuterococone is better developed, so that P^3 more nearly resembles P^4 .

In P^4 the primary or outer cusp and the deuterococone are about equal in height or vertical dimension, but there is no tritococone and no evidence of an hypocone. The outer cusp is conical but with anterior and posterior crests to the styles, whereas the deuterococone is acutely crescentic with its crests also joining the anteroexternal and posteroexternal styles. In one instance (Bridger) an accessory cuspsule was noted on the anterior crest. In addition to the crests of the deuterococone there is an anterior cingulum, which may be very weak, and a generally much stronger posterior cingulum. These tend to join the crests laterally before reaching the styles. The cingulum generally appears discontinuous across the lingual wall of the deuterococone, but may be weakly defined. The cingulum on the outer wall may continue across the outer rib of the primary cusp somewhat better defined than in P^3 . There is rather less to distinguish between earlier and middle stages of the Eocene in the character of P^4 , except that in the later stages the tooth often appears somewhat more compressed anteroposteriorly, with weaker styles.

The upper molars are low crowned bunodont teeth and the anterior two are nearly quadrilateral with six well-defined cusps. M^1 and M^2 are much alike except that the larger second molar is wider transversely and the outer margin is slightly more oblique. M^3 is more askew. In the first two the conical paracone and metacone are of equal size and joined together and to the anteroexternal and posteroexternal styles by a thin crest which in occlusal view is a nearly straight line, except at the styles where there is a sharp but very short outward flexure, and where this crest joins the prominent outer cingulum. There is no mesostyle. Lingually the protocone has about the same height as the outer cusps, but appears larger, exhibiting a more obtuse conical form tending to be somewhat crescentic. An anterolateral crest from the protocone joins the small protoconule and then converges with the anterior cingulum near the anterolateral style. The anterior cingulum is well developed, and usually somewhat crested anterior to the protocone where it may be slightly cuspsate. Pos-

teriorly, the protocone shows a small crest to the smaller and also slightly crescentic hypocone in the early and the middle Eocene stages. The posterolateral crest of the hypocone ascends to form the posterior cingulum, continuing laterally to the style. There is no cingular crest lingual to the hypocone although it may be weakly traced around the lingual margin of the protocone. The metaconule is a small, isolated cone about midway between the protocone and metacone in the early and middle Eocene stages. In the late Eocene the metaconule has become aligned with the hypocone, and the latter cusp is relatively a little larger and more widely and deeply separated from the protocone, giving the first and second upper molars a more lophodont appearance.

In M^3 the outer wall is decidedly oblique and the metacone generally a little smaller than the paracone. The anterior portion of the tooth is much as in the first two molars but posteriorly the hypocone is much less developed and often little more than a crested posterolingual portion of the cingulum. In the upper Eocene this crest may form a prominent posterolingual angle to the tooth, but is not joined with the metaconule as in the anterior molars.

Lower dentition.—The lower incisors are slender and with very elongate roots. In an arcuate arrangement they are decidedly procumbent, although decreasingly so toward the canine. The first is a little smaller than the second and both have narrowly spatulate crowns, occluding at a high angle with the broad posterior bevel of I^1 . I_2 also occludes laterally with the anterior margin of I^2 . The labial surface of each is gently convex in both directions, but the lingual surface has a strong longitudinal rib which is slightly concave in profile. The nearly parallel and somewhat compressed lateral margins turn lingually near the base of the crown to form a weak posterior (lingual) cingulum. I_3 has a somewhat shorter, more tapering crown than I_2 with a little broader base but a smaller, more nearly circular root. Its occlusion is with the posterointernal surface of I^2 and the anterior margin of I^3 .

The lower canine and P_1 are much like I_3 with a relatively simple, tapering crown, and a single circular root, but appear somewhat more erect, and C is distinctly larger. The base of the crown in these extends forward and upward so that the shorter, arcuate anterior crest is more outstanding than the straight to slightly concave posterior margin. A weak cingular crest may be developed lingually, at least in the posterior portion, and at its union with the posterior crest a small style is indicated for P_1 .

P_2 , as well as being larger than P_1 , is more elongate and relatively broader posteriorly. The anterior crest is strongly developed and

turns decidedly inward as it descends to join the prominent lingual cingulum. Posterolingually the cingulum becomes shelf-like and develops a slight crest as it turns outward and upward to join the well-defined posterior crest of the primary cusp, often exhibiting a small cusplule at the posterior extremity. P_2 would appear to be invariably two-rooted in all the Wasatchian material observed, although in some instances this could not be verified without damage to the specimen. In the Bridger, however, with the noted shortening of the premolar series, P_2 of *H. paulus*, while not infrequently two-rooted, is often single-rooted and in many instances the roots are not completely fused, showing prominent inner and/or outer grooves. In *H. minusculus*, and upper Bridger *H. lepidus* as well, P_2 appears more frequently two-rooted or deeply grooved. In larger *H. despiciens* of the upper Bridger this tooth seems almost invariably single-rooted.

The anterior portion of P_3 is very much like P_2 , but posterolingually it shows development of a third crest to the cingulum. Progressively this exhibits a marked flexure or rudimentary metaconid on its lower part. In Wasatchian materials the posterolingual crest may be very weak or absent and the indication of a metaconid relatively slight or rare. In Bridger materials, however, this crest is generally much better defined and the metaconid or flexure of the crest in this position seems almost invariable, much lower on the tooth, however, than in P_4 . Posteriorly P_3 shows a usually distinct but variably developed shelf or talonid, turned upward at the posterior rim so that a small talonid basin is developed lingual to the posterior crest of the primary cusp. In some instances the talonid rim is slightly cusplate, in positions suggesting the hypoconid and entoconid. Possibly this was more rarely encountered in Bridgerian than in Wasatchian materials, as the development of a talonid in the lower premolars suffered somewhat in the shortening of the premolar series observed for the middle Eocene. It may be noted, moreover, that P_3 as well as P_4 is invariably two-rooted.

P_4 is larger and relatively broader anteriorly than P_3 , with a somewhat stronger, often more lingually directed anterior crest. It is distinctive in the development of the metaconid which is high, relatively lingual to the protoconid and generally well separated from it, giving the greater part of the tooth a decidedly trigonid appearance. The talonid is, as would be expected, better developed than in P_3 , and there is a prominent cusp where the posterior crest from the primary cusp or protoconid joins the strong posterior cingular crest. These crests form a better defined talonid basin lingually than in P_3 , and generally there is a slight cingular shelf both posteroexternally and anteroexternally. It is interesting to note that within Wasatchian time there

appears to be progressive development of the talonid of P_4 , that in general, but not invariably, exhibits a more elongate, cuspsate condition in the Lost Cabin stage. In the Bridger the relative shortening of the premolar series appears to have affected the talonid of P_4 perhaps somewhat more, with respect to the earlier Eocene stages, than was noted for P_3 . As a consequence there is a less clearly definable posterointernal cusp in the position of an entoconid than is often so well defined in the more elongate P_4 of the late Wasatchian Knight materials.

The *Hyopsodus* lower molars are rather distinctive teeth with comparatively high conical cusps tending toward a selenodont pattern. The trigonid portion consists essentially of two cusps, the protoconid and metaconid in a distinctly oblique arrangement. These are connected by a sharply descending or notched crest from the posterolingual wall of the protoconid. A similar crest from the anterior wall of the protoconid turns sharply inward and downward, tending to become nearly parallel to the posterior wall of the trigonid. In the earlier stages of Wasatchian time this anterior crest on M_1 , and occasionally on M_2 , may rise again lingually to join a small paraconid placed high on the anterior slope of the metaconid. In the later stages of the Eocene this anterior crest of the trigonid on M_2 and M_3 is directed a short distance anterolingually where generally it more abruptly abuts the hypoconulid of the preceding molar to form a somewhat better defined crest from the protoconid to the entoconid of the talonid ahead.

On the talonid portion of the anterior lower molars the hypoconid, which is about the same height as the protoconid, and the somewhat lower entoconid also show a slightly oblique transverse arrangement. The crests from the hypoconid, however, give this cusp a distinctly selenodont appearance. The anterolingual crest, or crista obliqua, extends directly to the metaconid, joining this cusp below its apex and adjacent to the posterolingual crest from the protoconid. This leaves a steeply descending crevice or valley to the outer margin of the tooth, well separating the protoconid and hypoconid. The posterolingual crest from the hypoconid extends directly to the anterolateral wall of the prominent, conical hypoconulid a little below its apex. The hypoconulid rises from the cingulum distinctly posterior to a line between the hypoconid and entoconid, closer to the entoconid and posterolateral to it. The entoconid is usually a nearly circular cone which may show a crest to the adjacent hypoconulid. These cusps appear more strongly joined and often closer together in the late

Eocene, and in *H. fastigatus* the entoconid is comparatively large. Anteriorly the entoconid is well separated from the metaconid where the talonid basin opens lingually. The metastylid noted by L. Russell (1965) for *H. fastigatus* is not uncommon in Bridger material, and has been observed very weakly developed in certain Wasatchian specimens. In the earlier materials there is also a tendency for a slight cuspule to be formed on the anterior slope of the entoconid. A slight cingular shelf is developed anteriorly on the molars, at least at the anterior angles, and may be seen posteriorly rising to the hypoconulid on either side. Also, though not always present, it may be slightly crested or serrate externally between the protoconid and hypoconid.

M₃ differs from the anterior molars only in the character of the talonid, which is more elongate and tapering, with a very large and posteriorly projecting hypoconulid, usually better separated from the hypoconid and entoconid, although it may form a crest with the entoconid, more usual in the Wasatchian materials, although noted in a specimen of *H. fastigatus*.

Deciduous upper premolars.—Upper milk teeth have been seen or recognized only in the Knight, upper Bridger, and Uintan materials. The best preserved is a sequence of three, Dp²–Dp⁴, belonging to *H. lepidus* (pl. 6, fig. 3). Dp² is a small, nearly triangular tooth with anterior, posterior, and lingual crests. The anterior crest is straight and terminates at the cingulum in a small stylar cusp. The posterior crest is slightly flexed or notched near its lower extremity. The lingual crest or angle is directed somewhat posteriorly and also may show a very small style at its basal extremity. A weak cingulum is exhibited anterolingually and externally. The posterolingual face of the primary cusp is flat and relatively smooth to the basal margin.

In Dp³ the primary cusp, though larger, is rather like that in Dp² and externally they look very much alike, except for a more prominent anterior style on Dp³. A correspondence to P⁴ is noted in the well-developed and crested deutercone, but in Dp³ the talon is decidedly askew. In contrast to the somewhat elongate outer portion the distinctly basined talon is anteroposteriorly constricted and deflected posterolingually. The anterior crest from the deutercone extends as the cingulum along the anterolingual margin of the tooth to the anterior extremity where it joins the prominent, outward deflected style.

Dp⁴ is decidedly molariform and might easily be mistaken for M¹. It differs from M¹, nevertheless, in being relatively a little narrower transversely in comparison with the length of the outer wall, and the lingual portion is also a little more constricted anteroposteriorly.

Moreover, both the lingual and labial cusps are somewhat compressed, giving them a distinctly more acute appearance. The outer pair are flattened transversely, whereas the compression of the inner pair follows the alignment of the crests. In the very limited material of *H. miticulus* and *H. lepidus* the compression of the lingual cusps is largely transverse, but in the upper Eocene this is more oblique as a proto-loph tends to form, and the hypocone, better separated from the protocone, appears more as a high crest of the cingulum, but sometimes with a slight crest to the metaconule.

Deciduous lower premolars.—Lower milk teeth have been observed in the materials from all but the earliest and latest stages of the Eocene. No doubt, however, they are as well represented as upper deciduous premolars in the late Eocene collections. Dp_2 is evidently two-rooted, from very limited evidence in the middle as well as early Eocene. I have observed the tooth itself only in *H. lepidus* where it is relatively small. It resembles larger P_2 in the same species, although the primary cusp seems projected somewhat more forward than in the permanent dentition, and the short anterior crest is notched for a prominent style that is joined by the well-developed anterolingual cingulum. There is a posterolingual as well as a posteroexternal crest on the primary cusp and a slight posterior cingular crest.

Dp_3 in *H. lepidus* is very much like Dp_2 but larger and relatively broader posteriorly, and the parastylid is defined more as a sharp inward flexure of the anterior crest. The triangular posterior surface of the primary cusp is essentially smooth with little or no evidence of a cingular crest below. In *H. miticulus* (pl. 6, fig. 4), Dp_3 is much more elongate with a more prominent style relatively high on the anterior crest. Posteriorly the two crests of the primary cusp appear to converge upward a little below the apex and there is a slight median crest, which below joins a better defined crest of the cingulum that extends between the lower extremities of the outer and inner crests. A Dp_3 seen of *H. paulus* is relatively short as in *H. lepidus* but the posterolingual crest shows a prominent flexure in the position of a metaconid about midway on its length. As in *H. miticulus*, the posterior cingulum is more crest-like and there is a median cusplule on the very small talonid.

Dp_4 , as noted for Dp_4^1 , is distinctly molariform. It is, however, more easily recognized by its slender elongate form, and is particularly characterized in comparison with M_1 by the relative elongation of the trigonid with its crescentic cusp arrangement. The anterior crest from the protocone sweeps widely forward and inward to a well-developed parastylid or paraconid, which, together with the posterior

crest to the metaconid, defines a trigonid basin broadly open lingually, much as the talonid basin. The much smaller trigonid basin in M_1 opens forward or may be closed. Dp_4 , moreover, is distinctly lower crowned than M_1 , and its roots, of course, are better separated and more divergent.

VERTEBRAE

Representation of a significant portion of the vertebral sequence is preserved in only one specimen. This is an individual of *Hyopsodus paulus* (USNM 23740). It includes the cervicals, an articulated series of 23 dorsolumbars (pl. 13, figs. 1-3), a separate sacral portion of four coalesced vertebrae, and the incomplete first two caudals. A number of ribs are preserved but none are complete, and many were isolated and not identified as to position. It would appear that the tubercle and capitulum blended or became coalesced at about the eleventh or possibly the twelfth position. Of the sternum only three somewhat flattened and moderately elongate elements, from the mid-section or mesosternum, were recognized.

Cervical vertebrae.—The cervical vertebrae are not short, but although somewhat telescoped posteriorly they appear, nevertheless, to decrease in length from the axis to the seventh. They are, for example, not nearly so shortened as in the hedgehog but have relative proportions more nearly as in a rabbit. A portion of the atlas vertebra was preserved attached to the skull in USNM 23740, but the transverse processes as well as the lower margin are missing. The top portion of the arch is missing or incomplete in nearly all the cervical vertebrae, but the third is seen to lack a spine; in an isolated seventh of another individual there appears to be very little development of a neural spine. Ventrally, however, there is a sharp median ridge or hypapophysis on the axis to at least the fourth cervical vertebra. Posteriorly this may be more subdued. The transverse processes, where visible, appear extended fore and aft, with that for the third projecting well forward beneath that of the axis, rather like *Sylvilagus*. In the fourth and fifth cervicals there is suggestion in broken surfaces of a separation posteriorly of the transverse process, above and below the posterior opening of the good sized vertebrarterial canal, into dia- and parapophyses. The upper of these appears to be short and knob-like. In the sixth cervical the upper process is broken off but the inferior lamella is extraordinarily developed, extending greatly fore and aft (see pl. 13, fig. 1). This would suggest rather strong development of the longus colli, which would correlate with the development

of the hypapophysis on the anterior cervicals mentioned above. The bending of the neck implied would possibly add to the indication of a rooting habit suggested by the relatively large I¹. Much of the seventh vertebra is obscured by crushing but the upper process, or transverse proper, is outstanding and somewhat compressed or flattened obliquely.

Dorsal vertebrae.—No doubt the most interesting feature of the dorsal or thoracic sequence is its number. This is found to be twenty in the *H. paulus* specimen at hand. Although equalled in certain rhinos and elephants, it is apparently exceeded only in the hyrax and two-toed tree sloths among living land mammals.

The spines of the anterior dorsals appear to be decidedly elongate, although the dorsal portion of much of this sequence is obscured in the matrix by a closely appressed scapula. Beyond the eleventh vertebra of the postcervical series the dorsal portions of the vertebrae were exposed to weathering so that most of the neural arches are not preserved. The facets for the tubercle of the ribs are deeply pocketed and laterally outstanding on the transverse processes of the first two or three vertebrae, and remain separate from the facet for the capitulum at least as far as the tenth, or possibly eleventh. The facets for the capitulum are clearly discernible on the ventrolateral margin of the centrum, fore and aft, to a rib position between the 19th and 20th. The metapophysis may be first distinguished on about the third dorsal. It is clearly evident as far as the sixteenth, but not preserved beyond this point. The centrum in the dorsal sequence maintains about the same length throughout. It is, however, decidedly shallow or relatively flattened dorsoventrally, except that the anterior seven or eight are somewhat more V-shaped, with a more pronounced median angle or hypapophysis.

Lumbar vertebrae.—The number of lumbar in *Hyopsodus* is not known, as the *H. paulus* series is incomplete following the third, or twenty-third postcervical. These three lumbar have decidedly flattened centra with a broad surface above forming the floor of the neural canal and a weak median ridge or hypapophysis ventrally. The transverse process on the first is very weakly developed but on the second and third, though broken off, appears anteroposteriorly elongate and directed noticeably downward. The neural arches are not preserved.

Sacrum and caudal vertebrae.—The very poorly preserved sacrum was found separate from the foregoing sequence, but of the same individual. It includes four elongate, coalesced vertebrae, but the first is not complete anteriorly so that the full number is not known. The coalesced outer extremities on the left side show at least a part

of the sutural surface for the ilium, which tapers backward from broad contact opposite the first to a position opposite the anterior part of the third element preserved. The last sacral element exhibits small, closely appressed postzygapophyses for articulation with the first caudal vertebra. Only two caudals were preserved, evidently the first and second, and these are badly damaged. Their length, however, is seen to be a little less than that of the last sacral element. The transverse processes are broken away, but the root portions suggest that they were strongly developed. The centra are narrow and not nearly so flattened as in the dorsolumbar region.

PECTORAL GIRDLE

Scapula.—Both scapulae, though rather poorly preserved, are included in the materials of the *H. paulus* skeleton (USNM 23740; see pl. 13, fig. 4). The size is a little larger than in the Douglass ground squirrel, and like it has an unusually well-developed spine. The height of the spine and its flare toward the ventral extremity are perhaps relatively greater than in this squirrel. The scapula is only a little shorter than in the European hedgehog but the spine is better developed throughout its length, and the acromion, though widely expanded, apparently does not project so far downward, nor is the metacromial process so elongate as in the hedgehog. The prescapular fossa is moderately expanded and slightly convex, although the coracoid border is very poorly preserved and its outline was determined largely by its impression on the rock matrix. The postscapular fossa is narrow, concave and much obscured by the posteriorward deflection of the crest of the spine. There is a very small coracoid process, separated by a suture or possibly just a groove from the anteromedial extremity or margin of the glenoid surface. The character of the spine is quite unlike that in the hedgehog, or in the rabbit, and would suggest relative importance of those portions of the trapezius and deltoideus muscles that have here their insertions and origins respectively. No doubt *Hyopsodus* had an active digging habit as well as rooting.

Clavicle.—An incomplete clavicle, presumably the medial portion from the left side, shows a strong curvature and the extremity exhibits an enlarged, outward facing rugose convexity. The shaft is essentially trihedral with well-rounded angles, which becomes somewhat narrower just short of the rugose extremity. Unfortunately neither the manubrium nor the tip of the acromion are preserved so that the nature of these articulations cannot be described.

HUMERUS

The *Hyopsodus* humerus, particularly as noted in a recently acquired specimen of *H. minusculus* (pl. 11, fig. 2) has somewhat the general form noted in *Citellus*, but the deltoid ridge, though less outstanding, is very much longer, with its flattened and slightly rugose distal prominence for the deltoid muscle somewhat beyond the middle of the shaft. This crest is not nearly so short and sharply flexed as in *Erinaceus*, nor does it exhibit anything like the knobby development seen in the gophers. In its lengthy extent the deltoid crest is much like that in *Meniscotherium*.

The proximal extremity, as seen in *H. paulus* (pl. 10, fig. 1), shows an anterolaterally much extended greater tuberosity, more so than in *Citellus* or *Erinaceus*, but much more constricted anteroposteriorly than in these forms. The greater tuberosity, however, is not nearly so well developed as in *Meniscotherium*. Presumably the supraspinatus was inserted along the short low crest of the greater tuberosity, relatively less significant than in *Meniscotherium* with the infraspinatus posterior to it. A depression on the posterior surface of the greater tuberosity, much like that in *Meniscotherium*, was assumed to be for the teres minor but may have included insertion of the infraspinatus above as well. The lesser tuberosity is not outstanding or projecting, appearing as a somewhat flattened but well-developed scar for the subscapularis, posteromedial to the head, adjacent to and at a sharp angle with its articular surface.

The distal portion of the humerus, known for *H. minusculus* and *H. lepidus* as well as for *H. paulus* (pl. 10, fig. 2) and *H. walcottianus* (see Matthew, 1915b, fig. 10), is relatively broad, due largely to the prominent inner condyle which exhibits a well-developed entepicondylar foramen. The prominence of the inner condyle surely denotes importance of the various flexor muscles of the carpus and digits having origin there, further emphasizing a digging capability. The outer condyle, for the extensors, etc., is less prominent but supports a supinator ridge which extends proximally nearly a third of the length of the shaft. The development of the supinator ridge is about as in *Erinaceus*, but perhaps a little more sharply defined. It is less conspicuous and less laterally flaring than in *Citellus*. Its development also is relatively a little less than in *Meniscotherium*. The trochlea, as in *Meniscotherium*, has an outstanding medial margin anteriorly and distally, and a posteriorly raised lateral margin which arises from the more central convexity or capitulum of the trochlea as it extends around toward the posterolateral side. This articular convexity for

the radius, on the anterior portion of the trochlea, seems more prominent than in the hedgehog and much better defined than in the ground squirrels and gophers. There is a broadly open supratrochlear foramen, evidently as a consequence of the prominently projecting anconeal process or anteroproximal margin of the sigmoid notch of the ulna, which it accommodates in extension of the forearm.

RADIUS

An essentially complete radius is known for *H. minusculus* (USNM 24891, pl. 11, fig. 3) and extremities for various individuals of *H. paulus* and *H. lepidus* (pl. 10, figs. 4 and 5). The shaft is seen to be relatively slender and slightly curved, increasing somewhat in diameter distally. The more slender proximal portion shows little or no evidence of a bicapital tuberosity, although there is a slight crest developed in this position on the *Meniscotherium* radius. The more distal portion of the shaft is rather flattened and the crest for the interosseous membrane is but weakly developed.

The proximal extremity shows an oval to nearly bilobed surface (pl. 10, fig. 4) for the trochlea of the humerus, which is deeply concave posterolaterally for the capitulum and the anteromedial portion is markedly deflected distally. The latter flexure participates with the coronoid portion of the sigmoid notch of the ulna in articulating against the prominent medial flange of the trochlea. The sigmoid profile of the proximal surface is much more pronounced than in either *Erinaceus* or *Citellus*, being more as in *Meniscotherium* although not so elongate.

The distal extremity is relatively rounded and the articular surface shows facets for the scaphoid and lunar and a low anteromedially placed styloid process. The anterior surface exhibits a broad, shallow groove for an extensor tendon, presumably the extensor digitorum communis, which is bound laterally by a short but distinctive ridge deflected toward the ulna and defining a sharper groove close to the flattened surface of articulation with the ulna. This small, sharper groove may well be for the tendons of an extensor digitorum lateralis and an extensor indicis. The posterior surface of the distal extremity is more evenly rounded. The grooves and ridge on the anterior surface are much as in *Meniscotherium*, but possibly less pronounced on the relatively somewhat more enlarged distal extremity of the *Meniscotherium* radius. The distal extremity, particularly the articular surface, has little or no resemblance to that in *Erinaceus*.

ULNA

The forearm in *Hyopsodus*, as in *Meniscotherium*, is relatively short in comparison with the length of the humerus. The total length of the ulna is actually a little less than that of the humerus. The *Hyopsodus* ulna, known in *H. minusculus* (pl. 11, fig. 3) and *H. lepidus*, as well as in *H. paulus* (pl. 10, fig. 3) and *H. walcottianus*, is surprisingly like that in *Meniscotherium*, except for somewhat greater curvature. Proximodistally the posterolateral margin of the ulna is more convex through the greater part of the length, and the distal third of this margin is a little more concave. As in *Meniscotherium*, the shaft is flattened in an anterolateral-posteromedial direction and maintains a distinctive width distally with only a slight taper. In *Erinaceus* and *Citellus* the shaft of the ulna is more slender and tapering distally, as well as relatively much longer. The distal crest defining the interosseous membrane medially is similarly developed, and on the lateral surface the shaft shows the elongate median concavity and the posterior bounding crest much as in *Meniscotherium*, which are considered related to extensors of the more median digits.

The proximal extremity has a well-developed olecranon with an expanded rugose surface for the triceps insertions. Moreover, the length of the olecranon gives good leverage for these extensors of the forearm. The development of the olecranon is rather like that in *Erinaceus*, as well as *Meniscotherium*, better developed than in *Citellus*. The sigmoid notch also shows resemblance to that in the hedgehog, but is possibly a little more convex transversely, with the articular surface extending a little farther proximomedially. Moreover, the aconeal process is much more protruding.

The distal extremity is moderately expanded from the narrowest part of the relatively wide shaft and shows a prominent styloid process (missing from USNM 23740 shown in pl. 10, fig. 3) which is the extremity of a small distolaterally directed, anteriorly flexed, semi-cylindrical form articulating with the cuneiform and pisiform of the carpus. In *Meniscotherium* the somewhat cylindrical articular surface is straighter and relatively blunter, whereas in *Erinaceus* it is more saddle-shaped, with the articulating surface extending well out onto the lateral surface of the styloid process. The inner surface of the distal extremity is somewhat flattened to slightly concave, whereas the outer or anterolateral surface is more generally convex, with a distinct groove extending down toward the styloid process. This groove may be for the tendon of an extensor carpi ulnaris. A weaker, more medial groove would appear to combine with that of the radius suspected

above as conducting the tendons of the extensor digitorum lateralis and extensor indicis.

MANUS

The *Hyopsodus* fore foot is known from material representing three of the Bridger species; *H. paulus* (USNM 23740; pl. 10, figs. 9-12), *H. lepidus* (AM 11959; pl. 10, figs. 6-8), and *H. minusculus* (USNM 24891; pl. 11, fig. 3). The carpals, unlike the tarsals, show a certain amount of overlap, about to the extent seen in *Meniscotherium*. They show perhaps slightly less compression proximodistally, but are not so elongate as in the phenacodonts. The lunar is separate from the scaphoid and there is no central. Articulation of the fore foot with the radius and ulna reveals that in a normal arrangement of the elements of the fore arm and foot the palm is turned somewhat inward rather than strictly pronate. No doubt considerable flexibility was achieved in the fore limb and foot. A tendency toward supination was noted also for *Meniscotherium* (Gazin, 1965, p. 20).

Scaphoid.—The scaphoid is one of the moderately large elements of the carpus. It is proximodistally short as in *Meniscotherium*, but the proximal surface has a more projecting convexity for articulation with the radius. Ventromedial to the radial articulation the scaphoid projects prominently ventrad. Its distal surface, except toward the dorsomedial margin, is somewhat less inflected, although showing definable facets for the trapezium and trapezoid. The distomedial portion of the scaphoid, in its more dorsal part, shows a small but conspicuous projection toward the magnum, which exhibits an oblique, triangular facet for articulation with the latter element. This process, though evidently always present, varies somewhat in size between individuals, and, as noted in *Meniscotherium*, is in the position of a central, were this element separate. Laterally the scaphoid articulates broadly with the relatively small lunar.

Lunar.—The lunar is comparatively narrow and much shorter dorsoventrally than the scaphoid. Its dorsal extremity is of moderate depth, about comparable to the scaphoid and cuneiform, but ventrally it rapidly becomes much thinner proximodistally. Its proximal surface is slightly convex dorsoventrally and the oblong or nearly rectangular facet for the radius covers essentially the entire surface of the lunar. Medially the lunar appears somewhat triangular to slightly arcuate with this surface evidently articulating for most if not its entire length with the scaphoid. The lateral surface is similarly triangular, slightly concave and articulates proximally with the cuneiform. More

distally the surface is tilted somewhat for articulation with the proximomedial margin of the unciform. The distal surface has a slightly lateral tilt and articulates with the magnum. This articulation is a little constricted dorsally by the distolateral projection of the scaphoid.

Cuneiform.—The cuneiform is an elongate, somewhat bilobate structure, nearly as large as the scaphoid. The greater part of the proximal surface medially has a transversely elongate and dorsoventrally decidedly concave articular surface for the ulna. Ventral and parallel to this there is a transversely elongate and slightly convex surface, more ventrally oriented, for articulation with the pisiform. Lateral to these the cuneiform projects prominently ventrad. The dorsoventrally convex medial extremity of the cuneiform articulates with the more proximal portion of the lunar for the entire length of the latter. The greater portion of the distal surface of the cuneiform, except for the ventrolateral prominence, shows a relatively large, gently concave articular facet for the unciform. The cuneiform shows a striking resemblance to that in *Meniscotherium*, but appears a little less flattened and relatively not so deep dorsoventrally.

Pisiform.—The pisiform is relatively large, much the largest element in the carpus. Its broad anterior extremity shows a large concave facet for the ulna above and a transversely elongate and slightly concave facet for the cuneiform below. The shaft is elongate and the ventral or posterior extremity is much enlarged. Both, however, are somewhat compressed transversely relative to the anterior portion. The length of the shaft and the vertical expansion of the ventral or posterior extremity surely denotes importance for such muscles as the flexor carpi ulnaris which would have insertion above and the abductor digiti quinti with origin below, for flexing and abducting at least the outer part of the manus.

Trapezium.—The trapezium is known in only two specimens, one of *H. paulus* and the other of *H. lepidus*. It is an irregularly shaped bone, relatively much less compressed transversely than in *Meniscotherium*, but fairly deep dorsoventrally on its medial surface, although narrowing ventrally. The proximal surface which articulates with the medial portion of the scaphoid is dorsoventrally elongate and appears to turn slightly distal ventromedially, below which the bone projects more ventrally than in *Meniscotherium*. The distal articular surface for the first metacarpal is somewhat broader ventrally and generally concave dorsoventrally, except along the posterior margin where it is slightly recurved, and turns to meet the converging proximal surface.

Trapezoid.—A single known trapezoid, belonging to *H. lepidus*, is seen to be relatively short proximodistally, except on the dorsal surface where a prominent lip is projected distally over the proximal extremity of the second metacarpal. The proximal surface of the trapezoid, which articulates with a more lateral portion of the scaphoid, is triangular in shape, with its broad arcuate margin dorsal, and gently concave dorsoventrally. The distal surface is also triangular and concave dorsoventrally, but noticeably convex transversely. The medial and lateral surfaces for articulation with the trapezium and magnum, respectively, are proximodistally narrow and posteriorly convergent.

Magnum.—The magnum is a rather distinctive bone and has been figured separately (pl. 10, fig. 6). It is a relatively narrow and highly arched element with its short proximal and somewhat dorsally facing surface divided by a longitudinal ridge. Medially this surface is touched by the distolateral projection from the scaphoid and laterally by the lunar. The lateral surface of the magnum is essentially quadrilateral in outline and anteriorly it shows its articular facet for the unciform. The medial surface of the magnum, however, shows along its distal and greater part an elongate somewhat concave surface for its articulation with the lateral margin of the base of the second metacarpal. The more proximal contact of the medial surface, with the lateral margin of the trapezoid, is more restricted dorsoventrally. The distal surface for articulation with the third metacarpal is relatively narrow and elongate, covering almost the entire length of the bone. It is concave dorsally and slightly convex ventrally. Though much like that in *Meniscotherium*, the magnum appears to be relatively a little less extended ventrally.

Unciform.—The only unciform recognized in the *Hyopsodus* materials is incomplete laterally, but is evidently one of the larger elements of the carpus. The proximal surface for articulation with the cuneiform is overall convex, reaching its highest point medially near the narrow facet along the medial margin for the lunar. The unciform, however, is relatively not so deep medially as in *Meniscotherium* and the proximal and distal surfaces do not seem to converge so sharply laterad. The distal surface is large, dorsoventrally concave, with little or no separation showing for articulations of the fourth and fifth metacarpals. The concavity, however, is not so strong as in *Meniscotherium*. The medial surface shows dorsodistally an oblique or somewhat laterally deflected facet tapering ventrally for the outer margin of the base of the third metacarpal. Proximal and in part more ventral to this is the larger facet for contact with the magnum.

Metacarpal I.—The first metacarpal is the smallest of the five, being a little less than half the length of the third. The proximal extremity is dorsoventrally constricted but relatively broad. It does not show any smooth or clearly defined facet externally for the base of the second metacarpal, but the proximal surface for articulation with the trapezium is dorsoventrally very convex and somewhat saddle-shaped, with a knob-like lateral portion. Evidently articulation with the trapezium was highly flexible. The shaft of this element is slender and the distal extremity narrow and oblique with a noticeable taper medially.

Metacarpal II.—The second metacarpal is about equal to the fourth in length and about 85 percent of the length of the third. The proximal extremity or base is moderately deep and obliquely truncate ventrally. The surface for articulation with the trapezoid is gently convex dorsoventrally and distinctly concave transversely. The upturned proximolateral margin shows an elongate facet for the magnum. This facet faces proximolaterally and is somewhat tapering ventrally. Distal to the facet for the magnum the base of the second metacarpal is deeply concave for articulation with the proximomedial portion of the base of the third metacarpal. The shorter medial margin of the base of the second metacarpal is arcuate but not clearly faceted for the first metacarpal. The shaft of the second metacarpal is sturdy and broadens somewhat distally to the distinctly wider distal extremity. The distal extremity is deep, prominently keeled ventrally and slightly tapering medially.

Metacarpal III.—The proximal extremity of the third metacarpal, the longest of the five, is dorsally broad, moderately deep, and the ventral margin is truncated at about a right angle with the relatively straight medial margin. The proximal surface for articulation with the magnum and the concavity in the base of the second metacarpal is nearly rectangular, convex dorsally, and very slightly concave ventrally. Transversely the portion of the surface for the magnum is weakly concave. The surface in general is decidedly oblique to the long axis of the shaft, having a distomedial slope. The base of the third metacarpal projects strongly laterad in its more dorsal part, exhibiting an oblique, ventrally tapering facet for articulation with the unciform. Distal to this the lateral surface of the base is deeply concave for articulation with a portion of the proximal surface of the base of the fourth metacarpal. The shaft of the third metacarpal broadens distally and the distal extremity is moderately deep, ventrally keeled and without taper laterally or medially.

Metacarpal IV.—The fourth metacarpal has about the size and sturdiness of the second, but because of the manner in which the proximal extremities tend to overlap laterally, the fourth extends distally a little more than the second, but not so far as the third. The proximal extremity is broad dorsally and somewhat narrower ventrally, and has a little less depth dorsoventrally than the third metacarpal. The proximal articular surface is rather generally convex, more so dorsoventrally, and with but slight distinction between the surface for the unciform and that for the lateral concavity in the base of the third metacarpal. The portion of the surface for the unciform is broader dorsally and that for the third metacarpal appears to be of rather uniform width. The base of the fourth metacarpal, somewhat as in the second and third, is deeply concave laterally, with an arcuate distolaterally facing concave facet for the base of the fifth metacarpal. As with the second and third metacarpals, the shaft broadens distally to a relatively wide distal extremity which shows a moderately deep, ventrally keeled articular convexity which has a noticeable taper laterad.

Metacarpal V.—The fifth metacarpal is about three quarters as long as the fourth, but is a little larger and much more robust distally than the first. The proximal extremity is relatively broad transversely and decidedly convex dorsoventrally. The transversely broader lateral portion of the proximal articular surface, which makes contact with the unciform, is about as deep medially as the lateral margin of the base of the fourth metacarpal but tapers abruptly laterad. The more medial surface for the concavity in the base of the fourth metacarpal is distomedially oblique, more convex and less extended than the outer. The distal extremity is only a little smaller than that in the fourth metacarpal and the articular convexity tapers laterally a little more.

Phalanges.—Identification of the various phalanges (pl. 10, fig. 12) as to position is very tentative, although there would appear to be some evidence to suggest that those with the relatively broader and dorsoventrally shallower proximal extremities belong to the fore foot. I am unable, however, to distinguish phalanges belonging to the second digit on one side from those of the fourth digit on the opposite side. The proximal phalanges of digits II to IV appear to be approximately two-thirds the length of the corresponding metacarpal, and the second phalanges in turn are about two-thirds the length of the first. In the first digit it may be noted that the proximal phalanx is nearer three-fourths the length of the metacarpal. Each becomes a little narrower and shallower distally. The distal phalanges, unlike those of *Menis-*

cotherium, are transversely compressed and decidedly unguiculate. Allocation of the shorter distal phalanges to the fore foot is highly tentative and based on their lesser depth dorsoventrally, although the first and second phalanges, unlike the metacarpals, are slightly longer than in the hind foot.

PELVIC GIRDLE

Significant portions of the *Hyopsodus* innominate bone have been observed only in *H. paulus* (pl. 13, fig. 5), included in skeletal materials of two individuals (USNM 17980 and 23740). As previously recorded (Gazin, 1965), this structure is elongate and slender. The ilium shows the arcuate and flaring dorsal margin as in *Meniscotherium*, but the gluteal or outer surface may be a little less concave. The anterior extremity is missing in the material at hand. The base or posterior portion is a little less trihedral in cross section, with the pubic border of the ilium much more subdued than in *Meniscotherium*. There is little or no evidence for an iliopectineal eminence on the pubic border, which is weakly developed in *Meniscotherium*. As in the latter the acetabular border dominates as the inferior margin of the ilium, and the anterior inferior spine of human anatomy on the acetabular border, immediately anterior to the acetabulum, which supports origin of the rectus femoris, is surprisingly well developed. The rectus femoris acts through the patella as an extensor of the leg, with comparatively low leverage as a flexor of the hip, permitting a strong thrust, such as in saltation, although the short limbs do not suggest the latter as a habit. This process for the rectus femoris is prominently developed in lagomorphs, particularly *Brachylagus*, and in squirrels. In contrast it is scarcely evident in *Erinaceus*.

The ischium is slender but possibly a little less elongate than in *Meniscotherium*, although not nearly so short as in *Erinaceus*. The ischial spine is moderately developed and markedly rugose along its superior margin anterior to the apex, and seems relatively a little larger than in *Meniscotherium*. This may have afforded origin for one of the abductors of the thigh. The ischial tuberosity and the incompletely preserved ramus of the ischium are prominently developed, supporting origin for various flexors and abductors of the leg. Much of the pubic bone is also missing but, as indicated by the preserved portion, this element is distinctly slender. The cotyloid notch in the acetabulum for the ligamentum teres is constricted but directed along the ischium much as in *Meniscotherium*.

FEMUR

Femora of *Hyopsodus* are known principally from material of *H. paulus* (pl. 12, figs. 1 and 2), although fragmentary portions were found in the immature material of *H. lepidus* included in this study. The straight or but slightly curved *Hyopsodus* femur is slender and elongate and the shaft somewhat flattened anteroposteriorly throughout the greater part of its length. The proximal extremity appears transversely narrow in comparison with the sturdier but rather similar *Meniscotherium* femur, as the head and slender neck do not extend medially so noticeably. The head is well rounded, more nearly spherical than in *Meniscotherium*, and the fossa for the ligamentum teres is centrally located, rather than marginal as in that genus. The greater trochanter, for insertion of a portion of the gluteus muscles, is prominent but relatively less robust than in *Meniscotherium* and does not project proximally beyond the head. The digital or trochanteric fossa, for insertion of the obturator muscles, is deeply excavated but is not so elongate as in *Meniscotherium*, and the trochanteric ridge extends to a more proximal position relative to the lesser trochanter. The lesser trochanter is not preserved in any of the *Hyopsodus* specimens at hand but the character of its basal portion suggests prominent though less elongate development than in *Meniscotherium*. The third trochanter is well developed on the compressed outer margin of the shaft of the femur and is surprisingly distal in position. It appears as a somewhat elongate, flattened projection of the outer crest, at least midway on the length of the shaft or slightly beyond. This position is much as in *Meniscotherium*, or perhaps a little more distal, and gives considerable leverage to the superficial gluteus for abducting the limb, and together with others, as the iliopsoas inserted on the lesser trochanter, in flexing the hip joint.

The distal extremity of the *Hyopsodus* femur is poorly preserved in all specimens at hand, except for a fragment associated with the type-material of "*Lemuravus*" *distans*. It shows a striking resemblance to that in *Meniscotherium* but the patellar groove may be relatively a little broader.

The femur in a general way resembles that in *Erinaceus*, particularly in the relatively flattened appearance of the shaft. The latter, however, is somewhat more curved and becomes relatively broader distally. The proximal portion in *Erinaceus* is narrower with the greater trochanter closer to the head. The trochanteric fossa is much shallower and more medially placed. The outer crest-like margin of the shaft is moderately projected into a decidedly elongate third trochanter, much more

proximal in position than in *Hyopsodus*. Distally the patellar groove is very much broader than in *Hyopsodus*.

TIBIA

A nearly complete tibia is known for *H. paulus* (USNM 23740, pl. 12, fig. 5), as well as the distal portions (Gazin, 1965) for this species and *H. walcottianus*. As noted for *Meniscotherium*, the *Hyopsodus* tibia is a little shorter than the femur, not "considerably longer" as believed by Matthew (1909b, p. 516). It is relatively slender and only slightly curved forward. The proximal extremity of the tibia exhibits the two subequal articular surfaces complete only in a tibial fragment belonging with the type-material of "*Lemuravus*" *distans* (= *H. paulus*). The medial, somewhat smaller surface, proximal to the greater part of the shaft, is relatively flat for the most part, though slightly concave transversely toward the spine, but the larger, outer condylar surface is decidedly convex anteroposteriorly. Between the articular surfaces for the femur, the spine of the tibia or intercondyloid eminence is prominent anteriorly, but otherwise damaged. The outer portion of the proximal extremity extends a considerable distance lateral to the shaft, and distolateral to the outer condylar surface is the anteroposteriorly somewhat elongate surface for the fibula. Laterally this surface is transversely convex but closer to the shaft it becomes concave or groove-like on the distal surface of the head. The proximal extremity closely resembles that in *Meniscotherium* but is a little less developed anteroposteriorly.

The proximal portion of the shaft is somewhat compressed transversely, but more rounded distally. In *Meniscotherium* the proximal half of the shaft is relatively deeper anteroposteriorly and transversely more flattened. Except for the transversely flattened proximal portion of the shaft, the *Erinaceus* tibia, with its co-ossified fibula, bears little resemblance to that in *Hyopsodus*. The cnemial crest in *Hyopsodus* is comparatively low proximally, more so than in *Meniscotherium*, but roughened where the ligamentum patellae would be attached. It shows, nevertheless, increasing prominence distally toward the middle of the shaft. Its two surfaces would likely be involved in a complex of muscles medially and laterally, its more distal prominence possibly significant for the biceps femoris and might correlate with the development of the ischial tuberosity. Perhaps the sartorius also extended this far on the medial side. Farther distally the crest becomes much subdued as it extends toward the internal malleolus. The medial surface of the shaft is gently convex anteroposteriorly throughout its

length. The lateral surface, however, has a broadly convex rib proximally which, as support for the interosseous membrane, becomes sharply acute in the midsection, but continues somewhat more bluntly again toward the distal extremity. In *Meniscotherium* this crest is acutely developed for the entire length.

The distal extremity of the *Hyopsodus* tibia is represented in *H. paulus* and *H. lepidus*, as well as *H. walcottianus*. The distal articular surface is an oblong or nearly oval-shaped surface decidedly oblique to the long axis of the shaft, although possibly not so much so as in *Meniscotherium*. It is gently concave anteroposteriorly across its short diameter, and transversely it is broadly concave toward the inner malleolus and unflexed to but very weakly convex in the lateral part. Unlike *Meniscotherium* there is almost no ridge for a trochlea of the astragalus. The medial malleolus extends distally a little beyond the articular surface for the astragalus. The medial surface of the distal extremity is irregularly flattened, whereas the lateral surface is more acute, representing the distal end of the ridge for the interosseous membrane. Unlike *Meniscotherium*, however, a facet for the fibula is not clearly defined.

FIBULA

The fibula is known in only three specimens of *H. paulus*. One of these (USNM 23740; pl. 12, fig. 5) is essentially complete. It is a fairly straight, rather slender and fragile appearing bone with much expanded extremities. The proximal extremity is decidedly flaring, relatively more so than in *Meniscotherium*, with an anterodistally extending ridge prominently developed. It is suggested that because of its prominence that possibly some part of the biceps femoris above may have been inserted here, as well as the collateral ligament. Antero-externally the prominence no doubt included origin of the peroneus longus, and medially the tibialis posterior. Proximomedially the extremity exhibits a somewhat elongate and transversely recurved surface for its articulation with the tibia. In lateral view the line of contact of this surface with the external condyle of the tibia is noticeably oblique and behind it there is a posteriorly directed knob, less prominent, however, than the anterior flare. Presumably a strong soleus muscle had its origin on the outer portion of this knob. The medial surface distal to the articular surface is slightly convex anteroposteriorly with but weak indication of a crest for the interosseous membrane. The external surface of the proximal extremity is distinctly concave between the anterior and posterior prominences.

The distal extremity of the fibula is expanded, but somewhat less so than the proximal extremity, more nearly comparable in relative size to that in *Meniscotherium*. It shows an anteroposteriorly broad external malleolus and an oblique surface for the astragalus. The lateral margin of the distal surface is turned outward, evidently for some articulation with the calcaneum, but this marginal facet tends to be anteroposteriorly convex rather than concave as in *Meniscotherium*. The lateral tubercle of the malleolus, that bounds the groove for the peroneus longus anteriorly, is prominent but somewhat more posteriorly directed than in *Meniscotherium*, and the peroneal groove though narrower is deep and well defined. The medial surface of the distal extremity is rounded and slightly roughened proximal to the astragalar facet and there is no evidence of a facet for the tibia. In *Erinaceus* it may be noted that the fibula is ankylosed to the tibia for about half its length, even more so in the rabbit, and in the ground squirrels there is a fairly lengthy adhesion.

PES

The hind foot structure is known from materials of *H. paulus* (pl. 12, figs. 4, 6-12) and *H. lepidus*, as well as *H. walcottianus*. The tarsals have the distinctly serial arrangement of the condylarths, such as in *Phenacodus*, *Meniscotherium*, and *Tetraclaenodon*, not overlapping as in the arctocyonids, nor anything like the "taligrade" structure seen in the tillodonts. The hind foot is very much like that in *Meniscotherium*, except for much less reduced first and fifth metatarsals, and the decidedly unguiculate distal phalanges.

Astragalus.—The astragalus (pl. 12, fig. 8) has a moderately elongate neck, perhaps a little less oblique than in *Meniscotherium*, and a transversely broad, well-rounded head for articulation with the navicular. Laterally the head may make contact with the cuboid but this must be very slight. Matthew (1915b) described an astragalar facet on the cuboid (see p. 69); such an articulation, however, is not evident on the head of the astragalus. Perhaps the most distinctive feature of the *Hyopsodus* astragalus is the absence of any appreciable trochlear groove on the surface for articulation with the tibia. Medially this surface is not raised into a crest but is gently rounded onto the adjacent portion of the medial surface, which makes a very obtuse angle with the dorsal tibial surface. Likewise the lateral margin of the trochlea is not raised as a crest but makes a sharp 90° angle with the outer surface that articulates with the external malleolus of the fibula. The distoventral angle of the surface for the

fibula projects prominently laterad. This supports the distolateral extension of the ectal facet on the ventral surface of the astragalus. The ectal facet, laterally on the ventral surface of the body of the astragalus, is obliquely elongate and deeply concave, and the relatively large oval sustentacular facet on the ventral surface of the neck is somewhat convex. Between these the groove for the interosseous ligament is deeply impressed. This terminates posteromedially in the ventral aperture of the astragalar foramen. The groove on the posterior margin of the astragalus for the flexor hallucis longus is broad and well defined and terminates above at the dorsal aperture of the astragalar foramen, in an indentation of the posterior margin of the tibial facet.

Calcaneum.—The calcaneum (pl. 12, fig. 10) is moderately elongate and the posterior portion, beyond the astragalar condyle, comprises about half the length of the bone. The shaft of the posterior portion is transversely compressed anteriorly but broadens posteriorly to a knob-like tuberosity. The posterior surface of the tuberosity is dorsoventrally convex and transversely somewhat oblique. Excellent leverage is afforded the tendo calcaneus (Achilles) in extending the foot. Anterior to about the midpoint of the calcaneum the astragalar condyle is situated diagonally across the dorsal ridge with its convex articular surface facing anteromedially and somewhat dorsally. This condyle does not project dorsally from the superior ridge so much as in *Meniscotherium*. A narrow convex facet along the anterodorsal margin of the astragalar condyle articulates with the distal extremity of the external malleolus. A decidedly prominent peroneal tubercle projects laterally from near the end of the ridge extending forward from the anterolateral extremity of the astragalar condyle. Ventral to this the groove for the peroneus longus is relatively broad and well defined. The sustentaculum, medial to the astragalar condyle and somewhat more anterior in position, extends prominently mediad. It appears relatively a little more expanded anteroposteriorly than in *Meniscotherium*, but not nearly so thick dorsoventrally. It exhibits a slightly concave, oblique oval facet for the astragalus, facing antero-dorsal and somewhat medial. The posteroventral surface of the sustentaculum is smooth and broadly grooved for continuation of the extensor hallucis longus. The articular surface on the anterior or distal extremity of the calcaneum, for articulation with the cuboid is more rounded, not so concave dorsoventrally and a little less oblique than in *Meniscotherium*.

Navicular.—The *Hyopsodus* navicular (pl. 12, fig. 9) is short proximodistally and the proximal surface is deeply concave for articu-

lation with the head of the astragalus. The dorsal and medial margins are evenly rounded and ventromedially the rim of the proximal concavity rises to an acute process, relatively lower, however, than in *Meniscotherium*. The lateral surface is more nearly straight and shows an oval facet for articulation with the cuboid, extending up on a low ventrolateral process of the proximal margin. The ventral surface is notched for the tendon of the posterior tibialis, bounded laterally by a small ventral knob. The distal surface of the navicular is faceted for articulation with the cuneiforms. The medial portion of the distal surface is generally convex, somewhat triangular in outline and articulates with the internal and middle cuneiforms. There does not appear to be any distinction or separation of the areas for these two. The surface for the external cuneiform, however, is slightly tilted proximally from the more medial surface. It is gently convex and more elongate dorsoventrally, and meets the lateral articular surface for the cuboid at a little less than a right angle.

Cuboid.—The cuboid (pl. 12, fig. 11) is a relatively elongate bone, possibly less so than in *Meniscotherium*, but with more of the dorsal surface exposed proximodistally. The proximal or calcaneal surface is nearly oval but with a short, straight medial margin. The surface is noticeably convex and distolaterally sloping, although not so much so as in *Meniscotherium*. The distal articular surface is nearly triangular or somewhat trilobed. The larger portion for the fourth metatarsal, which includes the two more median lobes, is gently concave dorsoventrally. The outer, more abbreviated area for the fifth metatarsal is nearly flat and has a more proximal slope ventrally. Both may show a short upward deflection at the ventral margin, suggesting sharp deflection of the lateral digits. Ventral to these facets the transversely directed peroneal groove is very deeply impressed, partially covered ventrally by a distally extending flange from about midway on the cuboid. This flange, however, is not nearly so rugged as in *Meniscotherium*. The medial surface of the cuboid shows two somewhat oval shaped facets broadly joined at a very obtuse angle. The more proximal of these articulates with the navicular and forms about a 90° angle with the calcaneal surface. Possibly it was this facet for the navicular that Matthew (1909b, p. 516) thought articulated with the astragalus, but this clearly does not happen in an articulated foot of *H. paulus* at hand. The more distal of the two facets on the cuboid, about midway on the medial surface, articulates with the proximal portion of the lateral surface of the external cuneiform. Two very small facets at the distal extremity of the medial surface of the cuboid also make contact with the external cuneiform.

Internal cuneiform.—The internal cuneiform (pl. 12, fig. 12) is a proximodistally elongate and transversely flattened bone, with its proximal portion in medial view a little narrower than the distal. The proximal extremity shows a narrow and longitudinally concave surface for articulation with the ventromedial portion of the navicular. This surface, moreover, is not so oblique or dorsally oriented as in *Meniscotherium*. The more elongate distal surface for articulation with the first metatarsal is also slightly concave but in a more nearly transverse direction. Most of the proximal half of the broad lateral surface is faceted for the middle cuneiform, but more distally I see no facet or evidence of an articulation with the second metatarsal.

Middle cuneiform.—The middle cuneiform is the smallest of the tarsal elements. It is proximodistally short and transversely narrow but with evidently a somewhat longer dorsoventral dimension. The quadrilateral dorsal surface is almost square except for the somewhat longer medial margin. The proximal and distal surfaces are dorsoventrally concave, but that for the navicular is more elongate and shows an upturned ventral extremity. The distal surface for the second metatarsal is broad dorsally but narrower and more rounded ventrally. It is also very slightly convex transversely. The medial surface shows an elongate, somewhat bilobed articular surface for the internal cuneiform, extending obliquely from the proximoventral angle to near the dorsodistal angle of the surface. On the lateral surface there is a narrow facet, somewhat deeper dorsally, along the proximal margin for articulation with the external cuneiform.

External cuneiform.—Of the two cuneiforms recognized, neither that for *H. walcottianus* nor that in the immature materials of *H. lepidus* are complete ventrally. The bone is much deeper proximodistally than the middle cuneiform. The proximal surface for the navicular is relatively broad and flat dorsally, but not represented ventrally. The distal surface that articulates with the third metatarsal is elongate and concave dorsoventrally. Its dorsal portion is transversely broad, but about midway ventrad the surface is markedly constricted by a lateral indentation. The medial surface is narrowly faceted along the proximal margin for contact with the middle cuneiform and immediately distal to this the surface is rather deeply pocketed. Close to the distal margin the medial surface shows two separate facets for lateral surfaces on the head of the second metatarsal. The lateral surface of the external cuneiform shows a large facet proximally for contact with the cuboid, and distally at the extreme dorsal and ventral angles are small facets, the ventral of which articulates laterally with the proximal extremity of the fourth metatarsal. The other facet is dorso-

ventrally convex and seems to contact both the fourth metatarsal and the middle cuneiform.

Metatarsal I.—The first metatarsal though small is probably more than half as long as the second. The proximal extremity shows a broad and dorsoventrally convex articular surface for the internal cuneiform. The base is somewhat expanded laterally and shows a large rugose area but no facet for articulation with the second metatarsal. The shaft is stout but tapers distally, and the ventral surface is decidedly concave longitudinally. The distal extremity is slightly enlarged and relatively deep dorsoventrally. The distal articular surface is well rounded, keeled ventrally, and noticeably tapering medially. Moreover, the distal margin in dorsal view is distinctly oblique to the long axis of the shaft.

Metatarsal II.—The second metatarsal, as noted in *H. walcottianus*, is only very slightly shorter than the third but does not project so far distally because of the proximodistal shortness of the middle cuneiform relative to the external cuneiform. The base is about the same width as the shaft proximally, but has a strong ventral projection. The proximal surface is dorsoventrally convex and slightly turned up laterally, noticeably so at the ventrolateral angle, beyond the extent of the middle cuneiform. The medial side of the base lacks articular facets but the lateral side shows two well-developed surfaces for articulation with the external cuneiform. Distal to these the base of the second metatarsal is not faceted for contact with the third metatarsal. The shaft of the second metatarsal is somewhat flattened dorsoventrally and broadens a little distally. The distal extremity is moderately deep and strongly keeled ventrally. It tapers medially somewhat and the distal margin is only slightly oblique to the shaft.

Metatarsal III.—The third metatarsal, as the second, distally complete only in the material of *H. walcottianus*, is a sturdy elongate element, the shaft becoming somewhat broader and perhaps more flattened distally. The base has about the same width as the more proximal portion of the shaft, but projects prominently ventrad. The proximal surface is dorsoventrally convex and has a slight tilt distally toward the medial side. It is broadest dorsally and about midway is sharply constricted by a lateral re-entrant, a configuration quite like that of the distal surface of the external cuneiform. The medial surface of the base is slightly rugose with but weak marginal indication of contact with the second metatarsal which extends more proximally. The lateral surface, however, is deeply excavated and shows a concave facet dorsally and a knob-like convexity ventrad articulating with the fourth metatarsal. The distal extremity is distinctly broader than the

base and moderately deep dorsoventrally. The distal articular surface is well rounded, ventrally keeled, and essentially symmetrical on the two sides.

Metatarsal IV.—The fourth metatarsal, as seen in the material of *H. walcottianus*, is a trifle longer than the third, but as a result of the position of the bases in the proximal articulations, the third extends slightly farther distally. It may be further noted that in a comparison of the fourth metatarsal with the fourth metacarpal in material of *H. lepidus*, sufficiently preserved to indicate relative lengths, it seems evident that the second to fourth metatarsals are appreciably longer and, possibly, a little less flattened through the shaft than the corresponding metacarpals.

The base of the fourth metatarsal, unlike the second and third, is slightly wider than the more proximal portion of the shaft. The shaft, however, broadens distally about as in the other two. The proximal surface, articulating with the cuboid, is dorsoventrally elongate, convex, and tapers slightly ventrad. There is a slight median constriction from the medial side but not so deep as the adjacent indentation on the proximal surface of the third metatarsal. The relative width of the base of the fourth metatarsal is effected largely by a prominent process dorsally on the medial side, somewhat distal, however, to the surface for the cuboid. It exhibits a convex facet, proximomedially facing, for articulation with the concavity in the base of the third metatarsal. Near the ventral extremity of the base the medial surface articulates with the third metatarsal, and more proximally with the external cuneiform. The lateral surface of the base is deeply concave and the arcuate proximal portion of this concavity is faceted for articulation with the fifth metatarsal, making a sharply acute angle with the surface for the cuboid. The distal extremity has about the proportions seen in the third metatarsal but with a slight taper laterally. It appears, however, to be a trifle wider than in the second.

Metatarsal V.—The fifth metatarsal is relatively unreduced, as compared with this element in *Meniscotherium*. It is about 50 percent longer than the first metatarsal and with larger extremities. It appears to be only a little shorter than the fourth metatarsal and about as sturdy. The proximal extremity is dorsoventrally (dorsolateral-ventromedially) compressed and decidedly broad. Centrally on the proximal surface there is an oblique, slightly convex surface that turns up posteriorly and articulates with the outer part of the distal surface of the cuboid. Medial to the surface for the cuboid there is a more convex and proximomedially facing facet for the concavity on the base of the fourth metatarsal. Most noticeable on the base of the

fifth metatarsal is a very prominent ventrolateral process which, no doubt, supported insertion of the peroneus brevis, significant in evert-ing the foot as well as flexing the tarsus. The shaft of the fifth metatarsal is relatively straight along its dorsomedial border but the ventrolateral margin is decidedly concave. The distal extremity is enlarged and relatively deep. Its articular surface is only slightly oblique and much less tapering than on the first metatarsal.

Phalanges.—As noted in the discussion of the fore foot, the first phalanges of the hind foot appear to be somewhat narrower and deeper proximally than in the fore foot, and their length might be slightly less. The second phalanges also appear to be slightly shorter but their width does not taper distally so much as in the fore foot, giving further credence to the suggestion that the larger claw-like distal phalanges (pl. 12, fig. 4) belong to the hind foot.

SUMMARY OF RELATIONSHIPS

As noted in the introductory remarks, interpretations of relationships for *Hyopsodus* have been nearly as varied as for *Meniscotherium*. First described by Leidy as probably allied to the suillines, which accounts for his selection of the name (hog-aspect-tooth), it was also thought to be related to perissodactyls, proboscideans, and notoungulates. It was long regarded as a primate and an insectivore in turn, and then, as a result of the more detailed studies of Matthew, was later properly allocated to Cope's Condylarthra, a position further supported by Simpson (1945) in his classification of the mammals. Its closest relatives are, of course, the several genera that have been included with it in the family Hyopsodontidae, all of which, except for *Hyopsodus*, are Paleocene, although *Haplomylus* extends into the early Eocene. Only of *Hyopsodus*, however, is any significant representation of the skeleton known, other than jaws and teeth. Comparison of limbs and feet, as well as of skulls, is limited for this reason to the previously better documented materials of genera in the closely related condylarthran families Phenacodontidae and Meniscotheriidae. Detailed comparisons of the genera *Meniscotherium*, *Phenacodus*, and *Hyopsodus*, so far as then known, were made in 1965 and much of the expanded discussion of *Hyopsodus* in this paper relates to comparisons made with *Meniscotherium*, which on limb and foot structure appears a little closer than *Phenacodus*. While all three are rather similar in carpal and tarsal arrangement, unguiculate *Hyopsodus* is rather less like subungulate *Phenacodus*, and shows a different direction of development than indicated by the elongate hind foot structure recorded for

Tetraclaenodon. In cheek tooth structure *Hyopsodus* more nearly resembles or parallels *Ectocion*, among phenacodonts, except for the obvious difference in styler development and character of the upper premolars. A difference in food getting habit is seen in the relatively larger upper canines in *Ectocion*, instead of the anterior incisor. The skull of larger *Ectocion*, moreover, is relatively much broader. I have earlier (Gazin, 1956a, pp. 10-12) described a partially preserved skull of *Ectocion*, but postcranial material is very scant.

Although there is no authentic record of *Hyopsodus* in the early Tertiary of Europe, as discussed in a preceding section of this study, it may be noted that D. E. Russell (1964) has described the new Condylarthra *Paschatherium* and *Louisina* which he included in the Hyopsodontidae. These are represented in the early Eocene of Belgium and the late Paleocene of France. The type of *Paschatherium*, *P. dolloi* of Dormaal, was originally described by Teilhard de Chardin as a species of *Adapisorex*. Russell regards this as showing a closer resemblance to *Haplaletes* of the North American Fort Union, and which may be near its line of descent. These forms are not, however, especially close to *Hyopsodus* itself. The condylarthran affinities of the Cernaysian *Pleuraspidotherium* have been discussed (Gazin, 1965, pp. 85-88) at length in comparisons made with *Meniscotherium*.

A rather closer approach to *Hyopsodus* seems evident in certain of the South American Condylarthra. Paula Couto's (1952) allocation of *Asmithwoodwardia*, as recognized in material from the Paleocene at São José de Itaboraí, to the Hyopsodontidae has been noted and its resemblance to *Hyopsodus* is impressive, although cuspsation of the upper premolars, the position of the hypoconulid, and the extension (anteroposteriorly) of the trigonid in lower molars are rather distinctive. The procumbent arrangement of the lower incisors is suggestive, but the canine though small is relatively larger than in *Hyopsodus*. Also there appears to be more disparity between the canine and first premolar in both size and shape. Pascual's (1965) *Oxybunotherium* from the Casamayoran beds in Chubut, which was referred tentatively to the Didolodontidae, in many ways looks even more like *Hyopsodus*. This is suggested in the anteroposteriorly shortened trigonid of the lower molars, apparently lacking a paraconid, and the oblique trigonid crest. The arrangement of the cusps on the talonid is also rather similar to that in *Hyopsodus*. *Didolodus* itself is generally regarded as more distinctly phenacodont in appearance. The resemblance of *Anisolambda* to *Meniscotherium* has been discussed (Gazin, 1965, p. 83).

Among other groups that have been assigned to the Condylarthra I find *Hyopsodus* least like the Periptychidae. The tendency there toward inflation and/or proliferation of cuspsules in certain groups is quite opposite to that in *Meniscotherium*, and *Hyopsodus* preserves a more primitive or simple cuspsate arrangement, but only slightly crescentic or lophodont. The periptychid foot structure is rather different from that in *Hyopsodus*, exhibiting the peculiar astragalar articulation in the hind foot characteristic also of *Pantolambda*, and a central in the fore foot, not present in *Hyopsodus*, *Phenacodus*, or *Meniscotherium*. Inclusion of the periptychids in the Condylarthra has never been a completely satisfactory arrangement.

The arctocyonid creodonts, while showing a basic resemblance to the Condylarthra in the more primitive features of the molar structure, are probably closer than other groups outside the order and their adaptive specialization distinguishing them from the condylarths may well have been pre-Tertiary in origin. Their feet, moreover, are not truly of the condylarthran type, with overlapping tarsal elements, particularly the astragalus and cuboid.

The suggestion that tillodonts are condylarths is, of course, unwarranted, and derivation from any of the claeodonts is in no way demonstrated. Resemblances are not greater than may be seen between several of the orders of mammals in the early Tertiary. I suspect that convergence with the pantodonts in still earlier times is more likely, although premolar development has proceeded along quite different lines. Their foot structures, moreover, are rather similar, certainly not condylarthran. It also has been advocated that the mesonychid creodonts are condylarths. This stretches the concept of an order quite beyond orderly limits.

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EXPLANATION OF PLATES

PLATE 1

Hyopsodus paulus Leidy

Skull (USNM 17980), dorsal, lateral, and ventral views. Twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 2

Hyopsodus miticulus (Cope)

1, Rostral portion of the skull (USNM 23746), dorsal view. Twice natural size. Knight member, Wasatch formation, Green River Basin, Wyoming. For explanation of abbreviations see p. 90.

Hyopsodus paulus Leidy

2, Rostral portion of skull (USNM 17421), dorsal and lateral views. Twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

Hyopsodus minusculus Leidy

3, Rostral portion of skull and mandible (Webb School of Calif. coll.), lateral view. Twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 3

Hyopsodus paulus Leidy

Cranial portion of skull (USNM 23084), ventral, dorsal, and lateral views. Twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming. For explanation of abbreviations see p. 90.

PLATE 4

Hyopsodus paulus Leidy

1, Skull (USNM 23740), lateral and ventral views.

2, Skull (USNM 17980), occipital view.

Twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

Hyopsodus miticulus (Cope)

3, Cranial portion of skull (USNM 23745), occipital view. Twice natural size. Knight member, Wasatch formation, Green River Basin, Wyoming.

PLATE 5

Hyopsodus miticulus (Cope)

- 1, Endocranial cast (USNM 23745), dorsal and lateral views.
 - 2, Cranium (USNM 23745), lateral and dorsal views.
- Twice natural size. Knight member, Wasatch formation, Green River Basin, Wyoming. For explanation of abbreviations see p. 90.

PLATE 6

Hyopsodus paulus Leidy

- 1, Palatal portion of skull (USNM 23747), lateral and ventral views (Left P¹ restored to normal position in occlusal view).
 - 2, Endocranial cast (USNM 23747), ventral view.
- Twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming. For explanation of abbreviations see p. 90.

Hyopsodus lepidus Matthew

- 3, Left upper milk teeth, Dp²-Dp⁴ (AM 11959), occlusal view. Twice natural size. Twin Buttes member (C), Bridger formation, Green River Basin, Wyoming.

Hyopsodus miticulus (Cope)

- 4, Right lower milk teeth, Dp₃-Dp₄ (USNM 19606), occlusal view. Twice natural size. Knight member, Wasatch formation, Green River Basin, Wyoming.

PLATE 7

Hyopsodus despiciens Matthew

- 1, Skull (AM 11877), part of type-specimen, lateral and ventral views. Natural size.
 - 2, Left ramus of mandible (AM 11877), part of type-specimen. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size.
- Henry's Fork, Twin Buttes member (D), Bridger formation, Green River Basin, Wyoming.

Hyopsodus lepidus Matthew

- 3, Left ramus of mandible (A.M. 11900), part of type. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size.
- Henry's Fork, Twin Buttes member (C), Bridger formation, Green River Basin, Wyoming.

Hyopsodus paulus Leidy

- 4, Right ramus of mandible (USNM 1176), type-specimen. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size.
- Near Fort Bridger, Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

Hyopsodus vicarius (Cope)

- 5, Fragment of right ramus of mandible (AM 5004), one of original cotypes. Lateral view natural size. Occlusal view of posterior two molars twice natural size.

- 6, Fragment of left ramus of mandible (AM 5003), type-specimen (lectotype). Lateral view natural size. Occlusal view of first lower molar twice natural size.

Cottonwood Creek, Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 8

Hyopsodus walcottianus Matthew

- 1, Upper cheek teeth (AM 14654), part of type.
- 2, Right ramus of mandible (AM 14654), part of type.
- 3, Left ramus of mandible (AM 14654), part of type.

Lateral views natural size. Occlusal views of cheek teeth twice natural size. Alkali Creek, Lost Cabin member, Wind River formation, Wind River Basin, Wyoming.

Hyopsodus browni Loomis

- 4, Upper cheek teeth (AC 3242), part of type.
- 5, Left ramus of mandible (AC 3232), part of type. Lateral view natural size.

Occlusal views of cheek teeth twice natural size. Bridger creek, Lysite member, Wind River formation, Wind River Basin, Wyoming.

Hyopsodus jacksoni Loomis.

- 6, Upper cheek teeth (AC 3470), part of type.
- 7, Right ramus of mandible (AC 3246), part of type. Lateral view natural size.

Occlusal views twice natural size. Bridger Creek, Lysite member, Wind River formation, Wind River Basin, Wyoming.

Hyopsodus powellianus Cope

- 8, Right ramus of mandible (AM 4147), type-specimen. Lateral view natural size. Occlusal view of lower molars twice natural size. Will-wood formation, Bighorn Basin, Wyoming.

PLATE 9

Hyopsodus marshi Osborn

- 1, Right and left upper cheek teeth (AM 1706a), type-specimen. Occlusal views twice natural size. Twin Buttes or Henry's Fork, Twin Buttes member (C or D), Bridger formation, Green River Basin, Wyoming.

Hyopsodus uintensis Osborn

- 2, Upper cheek teeth (AM 2079), type-specimen. Occlusal view twice natural size. White River, Uinta formation, Uinta Basin, Utah.

Hyopsodus fastigatus Russell and Wickenden

- 3, Left second lower molar (NMC 8654), type-specimen. Occlusal view twice natural size. Swift Current Creek beds, Saskatchewan, Canada.

Hyopsodus loomisi McKenna

- 4, Right upper cheek teeth (UC 44781), type-specimen. Occlusal view twice natural size. Four Mile Creek, Wasatch formation, Washakie Basin, Colorado.

Hyopsodus lemoinianus Cope

- 5, Left ramus of mandible (AM 4139), type-specimen. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size. Willwood formation, Bighorn Basin, Wyoming.

Hyopsodus lysitensis Matthew

- 6, Portions of left ramus of mandible (AM 15621), type-specimen. Lateral views natural size. Occlusal views of lower cheek teeth twice natural size. 15 mile Creek, Willwood formation, Bighorn Basin, Wyoming.

Hyopsodus wortmani Osborn

- 7, Portions of right and left maxillae and premaxillae with upper teeth (AM 4716), part of type-specimen. Occlusal view twice natural size.
8, Left lower cheek teeth (AM 4716), part of type-specimen. Occlusal view twice natural size.
9, Right ramus of mandible (AM 4716), part of type-specimen. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size.

Probably Lost Cabin member, Wind River formation, Wind River Basin, Wyoming.

Hyopsodus simplex Loomis

- 10, Left ramus of mandible (AC 2290), type-specimen. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size. Gray Bull member, Willwood formation, Bighorn Basin, Wyoming.

Hyopsodus minor Loomis

- 11, Right ramus of mandible (AC 3492), type-specimen. Lateral view natural size. Occlusal view of lower molars twice natural size. Bridger Creek, Lysite member, Wind River formation, Wind River Basin, Wyoming.

Hyopsodus latidens Denison

- 12, Left ramus of mandible (MCZ 9848), type-specimen. Lateral view natural size. Occlusal view of posterior lower molars twice natural size. North Fork of Wind River, Indian Meadow formation, Wind River Basin, Wyoming.

Hyopsodus markmani Abel and Cook

- 13, Left upper Dp⁴ and M¹ (DMNH 486), part of type-specimen. Occlusal view twice natural size.
14, Right lower molar (DMNH 486), part of type-specimen. Lateral view natural size. Occlusal view twice natural size.

Middle Eocene deposits in Sand Wash Basin, Moffat Co., Colorado.

Hyopsodus distans (Marsh).

- 15, Right and left upper cheek teeth (YPM 12907), part of type-specimen. Occlusal views twice natural size.
16, Right ramus of mandible (YPM 12907), part of type-specimen. Lateral view natural size. Occlusal view of lower cheek teeth twice natural size.

Grizzly Buttes, Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 10

Hyopsodus paulus Leidy

- 1, Proximal portion of right humerus (USNM 23740), proximal (left above), medial (left below), posterior (middle), and lateral (right) views.
- 2, Distal portion of right humerus (composite USNM 23740 and 17980), medial (left), anterior (right above), and distal (right below) views.
- 3, Left ulna (USNM 23740), anterior (left), lateral (right), and distal (right below, restored) views.
- 4, Proximal portion of right radius (USNM 23740), proximal (above) and anterior views.

All twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

Hyopsodus lepidus Matthew

- 5, Distal portion of right radius (AM 11959, immature), posterior and distal (anteromedial margin down) views.
- 6, Left magnum (AM 11959), medial (left) and lateral views.
- 7, Right articulated distal carpals (AM 11959, unciform incomplete laterally), proximal view (left to right; unciform, magnum, trapezoid, and trapezium).
- 8, Right articulated carpals (AM 11959, lunar and pisiform missing, and unciform incomplete laterally); proximal view (upper figure, left to right; cuneiform and scaphoid with magnum of distal row partially exposed between), lateral view (figure to left, with cuneiform above and incomplete unciform below; scaphoid and magnum partially exposed), anterior or dorsal view (central figure; cuneiform and scaphoid, left to right, in upper row; and unciform, magnum, trapezoid, and trapezium left to right, in lower row), medial view (figure to right; scaphoid above and magnum, trapezoid, and trapezium left to right in lower row) and distal view (lower figure, left to right; incomplete unciform exposing part of cuneiform to left, magnum, trapezoid, and trapezium).

All twice natural size. Henry's Fork, Twin Buttes member (C), Bridger formation, Green River Basin, Wyoming.

Hyopsodus paulus Leidy

- 9, Left metacarpals I to IV (USNM 23740; Mc V missing), proximal view (left to right, IV to I).
- 10, Left carpals and metacarpals (USNM 23740; trapezium, trapezoid, unciform and Mc V missing; lunar and Mc III incomplete), proximal view (upper figure, left to right; scaphoid, lunar, and cuneiform partially concealed by pisiform), medial view (figure to left; scaphoid partially concealing pisiform, distomedial carpals missing), dorsal view (central figure; left to right above, scaphoid, lunar, and cuneiform partially concealing pisiform; only magnum, partially restored from AM 11959, represented in distal carpal row; below, left to right, metacarpals I to IV, metacarpal III incomplete and V missing), and lateral view (figure to right; cuneiform and pisiform left to right, with magnum partially exposed below).

- 11, Left articulated proximal carpals (USNM 23740), distal view (left to right, scaphoid, lunar, and cuneiform).
 - 12, Phalanges, probably all from third digit and believed to represent fore foot (USNM 23740), dorsal and lateral views.
- All twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 11

Hyopsodus minusculus Leidy

- 1, Skull with mandible (USNM 24891), lateral view.
 - 2, Left humerus (USNM 24891), lateral (left) and posterior views.
 - 3, Right radius, ulna, scaphoid, lunar, and metacarpals I to V (USNM 24891), anterior or anterolateral view of fore limb with dorsal view of fore foot (left), and medial or anteromedial view of fore limb with medial view of fore foot (right).
- Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 12

Hyopsodus paulus Leidy

- 1, Proximal portion of right femur (USNM 17980), anterior (left), proximal (right above), and posterior (right below) views.
 - 2, Distal portion of left femur (USNM 17980, distally restored from YPM 12907), anterior (right) and distal (left) views.
 - 3, Left patella (USNM 23740), anterior view.
 - 4, Phalanges, probably all from third digit and believed to represent hind foot (USNM 23740), dorsal and lateral views.
 - 5, Left tibia and fibula (USNM 23740); anterior (left), distal (left below), proximal (right above, restored from YPM 12907), and lateral (right) views.
- All twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

Hyopsodus paulus Leidy and *Hyopsodus lepidus* Matthew

- 6, Composite left pes; astragalus, calcaneum, navicular, cuboid, internal cuneiform and metatarsals I (reversed from right), III (incomplete), and V (reversed from right) of *Hyopsodus paulus* (USNM 23740, except Mt III, USNM 23748); middle cuneiform, external cuneiform (incomplete), and metatarsals II and IV (both incomplete and reversed from right) of *Hyopsodus lepidus* (AM 11959); dorsal view.
 - 7, Composite left metatarsals; I (reversed from right), III, and V (reversed from right) of *Hyopsodus paulus* (USNM 23740; except Mt III, USNM 23748); metatarsals II and IV (reversed from right) of *Hyopsodus lepidus* (AM 11959); proximal views.
- All twice natural size. Bridger formation, Green River Basin, Wyoming.

Hyopsodus paulus Leidy

- 8, Left astragalus (USNM 23740); lateral, ventral, and medial (left to right) views.
- 9, Left navicular (USNM 23740); proximal (above), medial (left), dorsal (center), lateral (right), and distal (below) views.
- 10, Left calcaneum (USNM 23740); medial, dorsal, and lateral (left to right) views.
- 11, Left cuboid (USNM 23740); proximal (above), medial, dorsal, lateral, ventral (left to right), and distal (below) views.
- 12, Left internal cuneiform (USNM 23740); distal, medial, lateral, and proximal (left to right) views.

All twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

PLATE 13

Hyopsodus paulus Leidy

- 1, Axis to second dorsal vertebra (USNM 23740), lateral view.
- 2, Third to thirteenth (right to left) dorsal vertebrae and rib portions (USNM 23740), ventral view of vertebrae.
- 3, Fourteenth to twentieth (right to left) dorsal vertebrae and three lumbar (USNM 23740), ventral view.
- 4, Right scapula (USNM 23740), lateral view (restored in part from left).
- 5, Left innominate bone (USNM 17980), lateral view (partially restored from right).

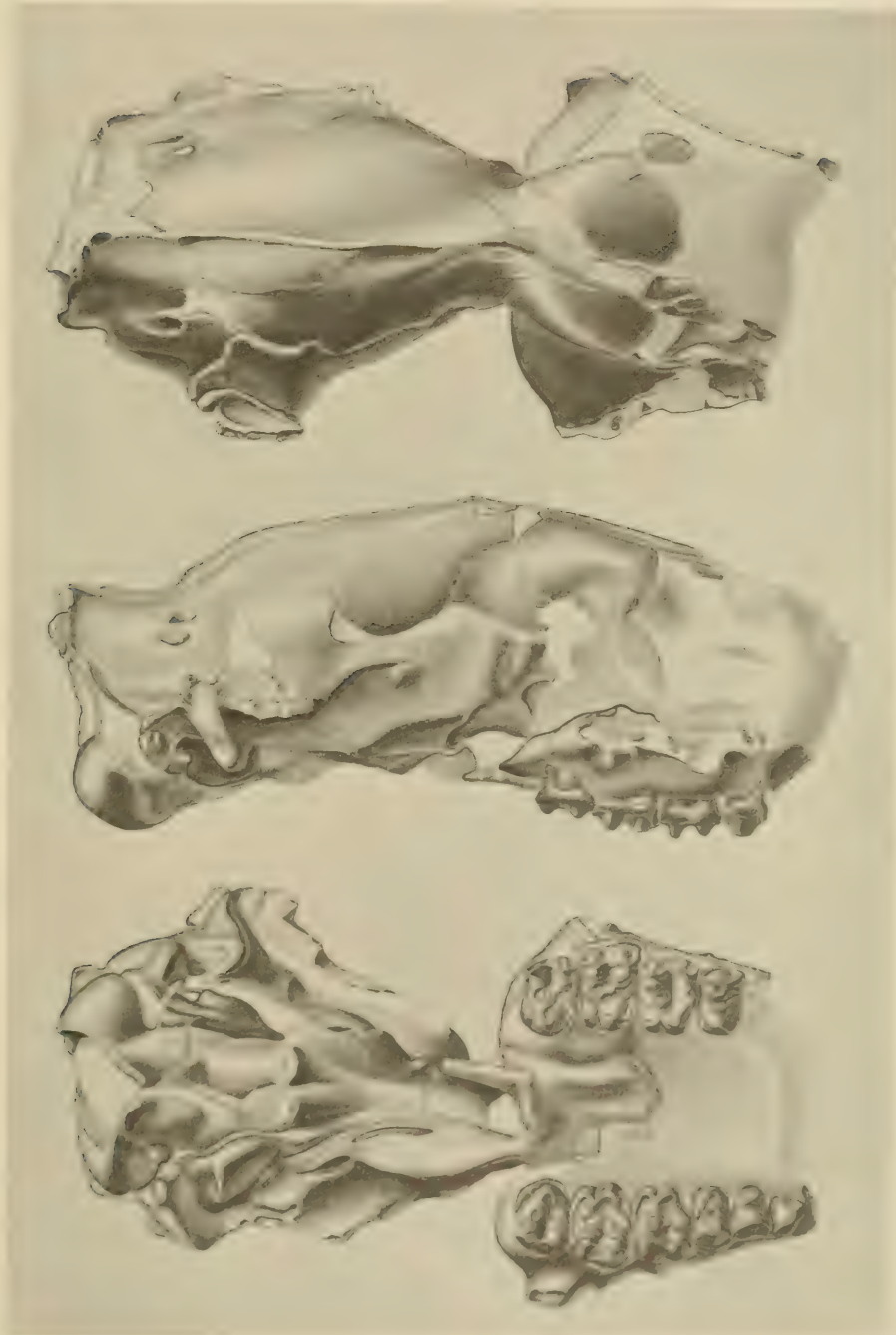
All twice natural size. Blacks Fork member (B), Bridger formation, Green River Basin, Wyoming.

EXPLANATION OF ABBREVIATIONS FOR PLATES

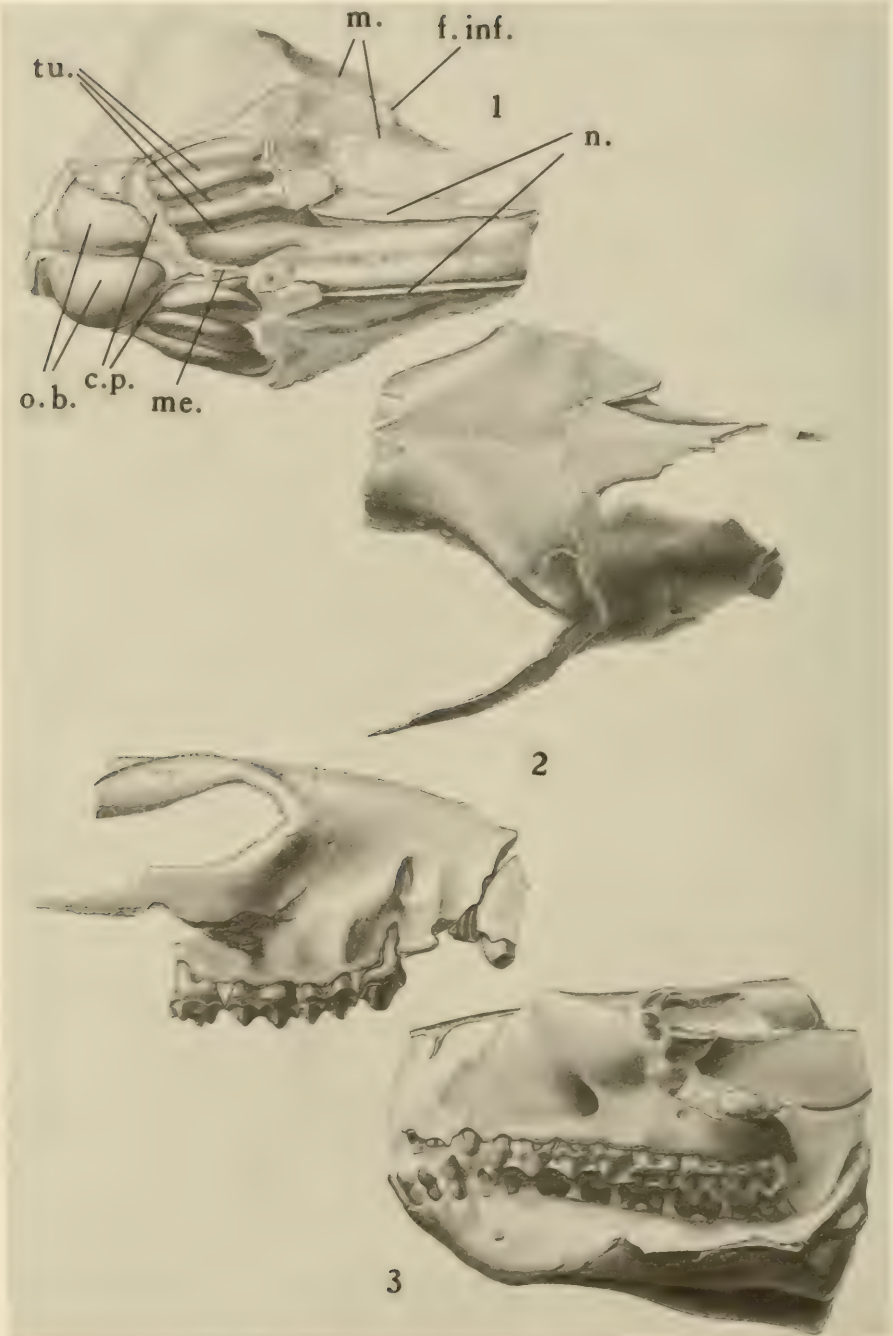
It is understood that the annotations as applied to casts refer to position and external form of soft parts, including their mantle, or representation of contents where the name applies to a boney structure, such as a foramen or sinus.

| | |
|----------------|--|
| a.c. | Anterior culliculi or corpora quadrigemina. |
| c. | Impression of broken surface exposing cochlea. |
| c.f. | Condylar foramen (incl. nerve XII and veins). |
| c.p. | Cribiform plate. |
| cav.s. | Cavernous sinus. |
| e.a.m. | External auditory meatus. |
| f.inf. | Infraorbital foramen. |
| f.l.m. | Foramen lacerum medium. |
| f.l.p. | Foramen lacerum posterius (incl. nerves IX, X, and XI, and internal jugular vein). |
| f.m. | Foramen magnum. |
| f.o. | Foramen ovale (incl. nerve V ₃). |
| fen.o. | Fenestra ovalis. |
| fen.r. | Fenestra rotunda. |
| fl. | Flocculus of cerebellum. |
| gl. | Glenoid surface. |
| hy. | Hypophysis |
| i.a.m. | Internal auditory meatus (incl. nerves VII and VIII). |
| i.p.s. | Inferior petrosal sinus. |
| ll. | Lateral lobe of cerebellum or cerebellar hemisphere. |
| lat.s. | Lateral or transverse sinus. |
| long.s. | Longitudinal or sagittal sinus. |
| m. | Maxilla. |
| m.o. | Medulla oblongata. |
| m.p. | Mastoid process. |
| me. | Mesethmoid. |
| n. | Remnants of inferior crests of nasals. |
| n.p. | Neopallium. |
| o.b. | Olfactory bulbs. |
| op.f. | Optic foramen. |
| p.c. | Posterior culliculi or corpora quadrigemina. |
| p.f. | Paramedian fissure. |
| p.gl.f. | Postglenoid foramen. |
| p.gl.p. | Postglenoid process. |
| p.l. | Pyramiform lobe. |
| p.p. | Paroccipital process. |
| s.p.s. | Superior petrosal sinus. |
| sph.f. | Sphenoidal fissure. |
| st.m.f. | Stylomastoid foramen. |
| tu. | Impressions of turbinals. |
| v.c. | Vermis cerebelli. |
| VIII | Aperture in facial canal for facial nerve. |
| V ₃ | Third division of trigeminal nerve. |

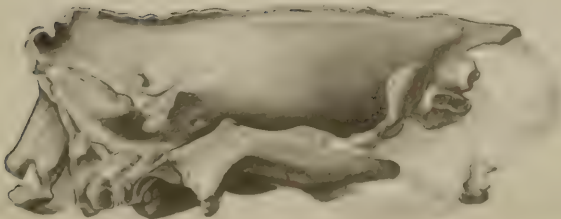
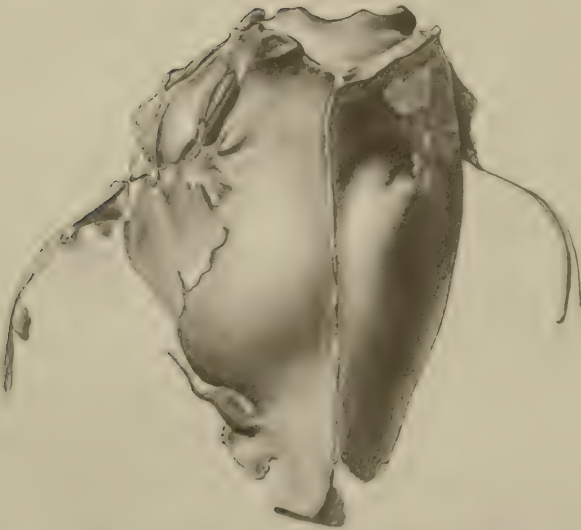
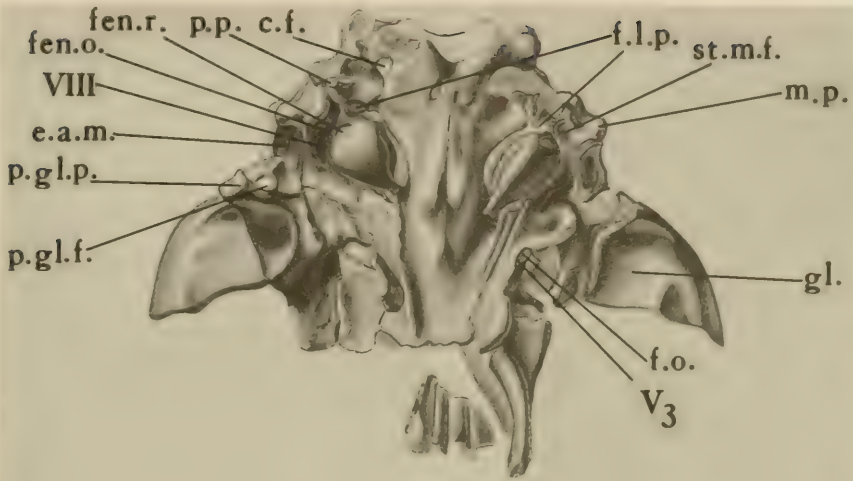
PLATES 1-13



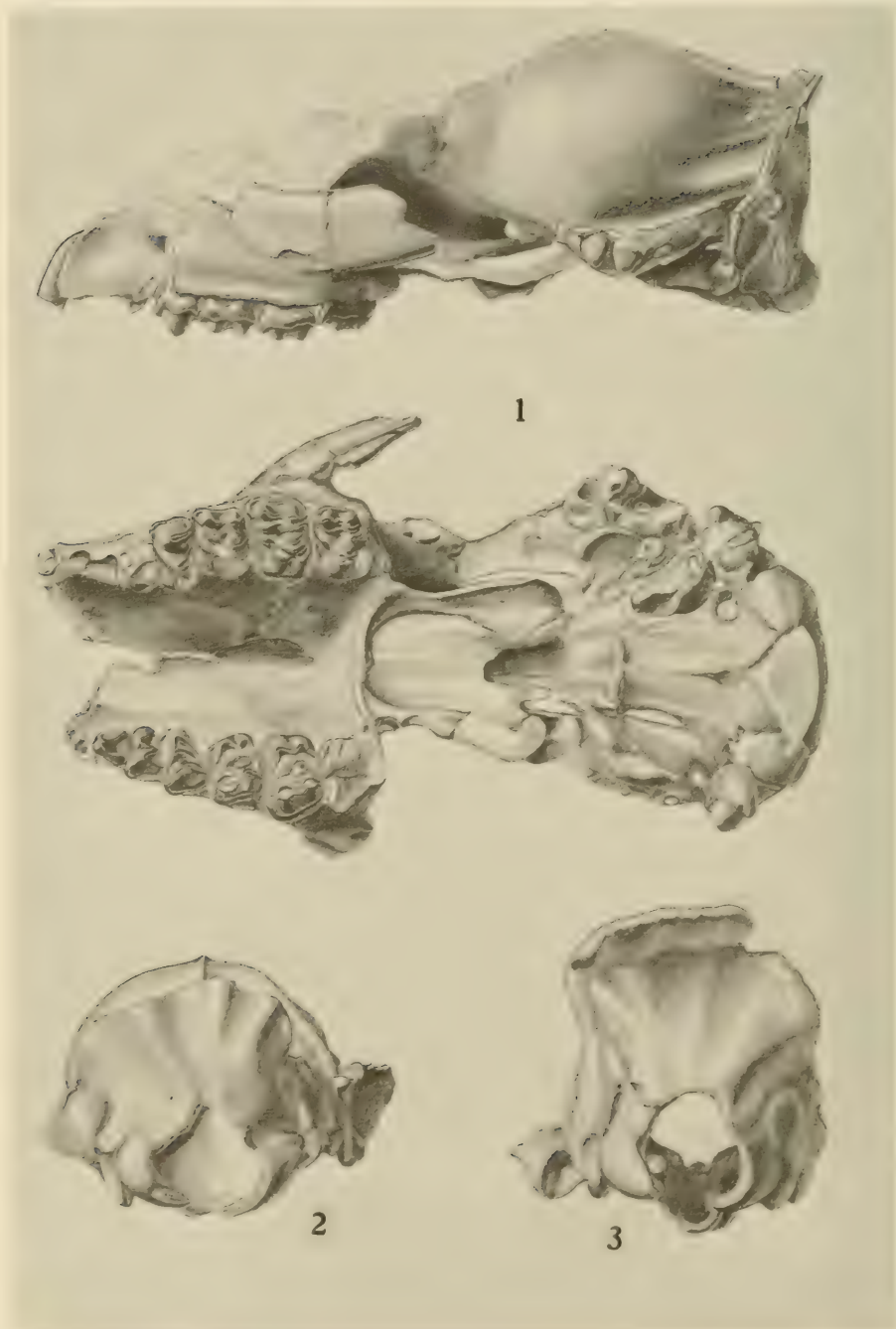
Hyopsodus skull from the middle Eocene of Wyoming
(See explanation of plates on pp. 83-90.)



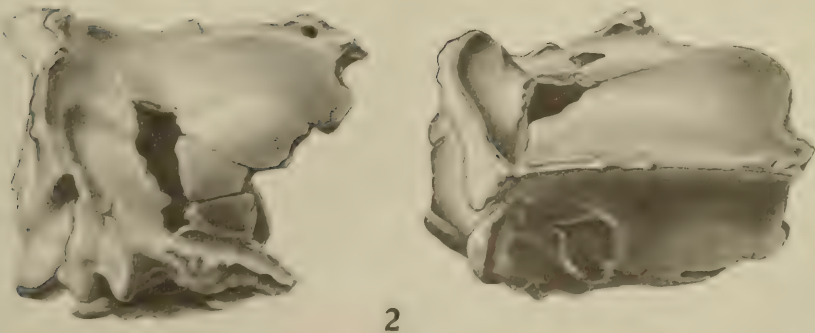
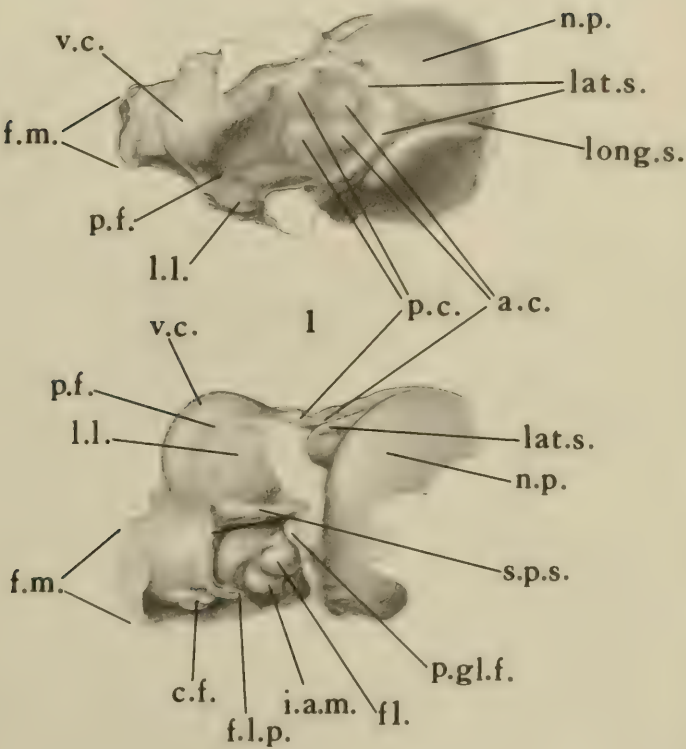
Hyopsodus skull portions from the early and middle Eocene of Wyoming
(See explanations of plates and abbreviations on pp. 83-90.)



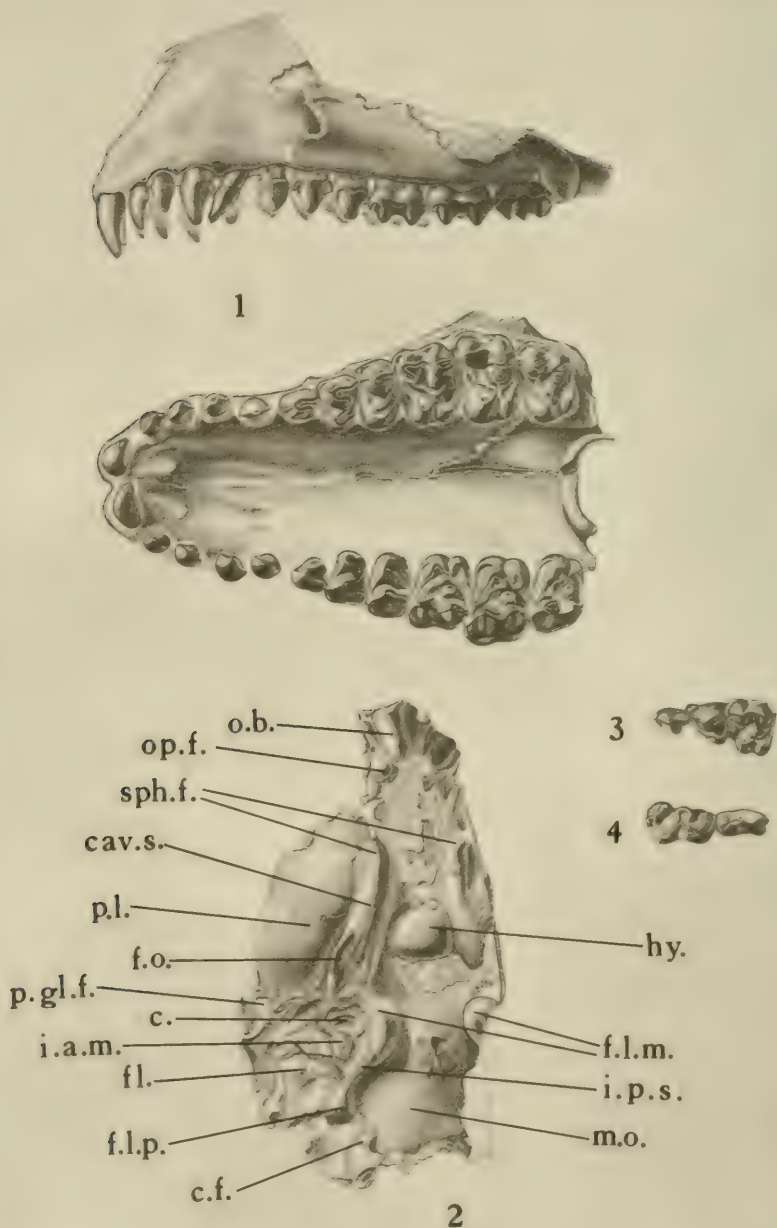
Hyopsodus skull portion from the middle Eocene of Wyoming
(See explanations of plates and abbreviations on pp. 83-90.)



Hyopsodus skulls from the early and middle Eocene of Wyoming
(See explanation of plates on pp. 83-90.)

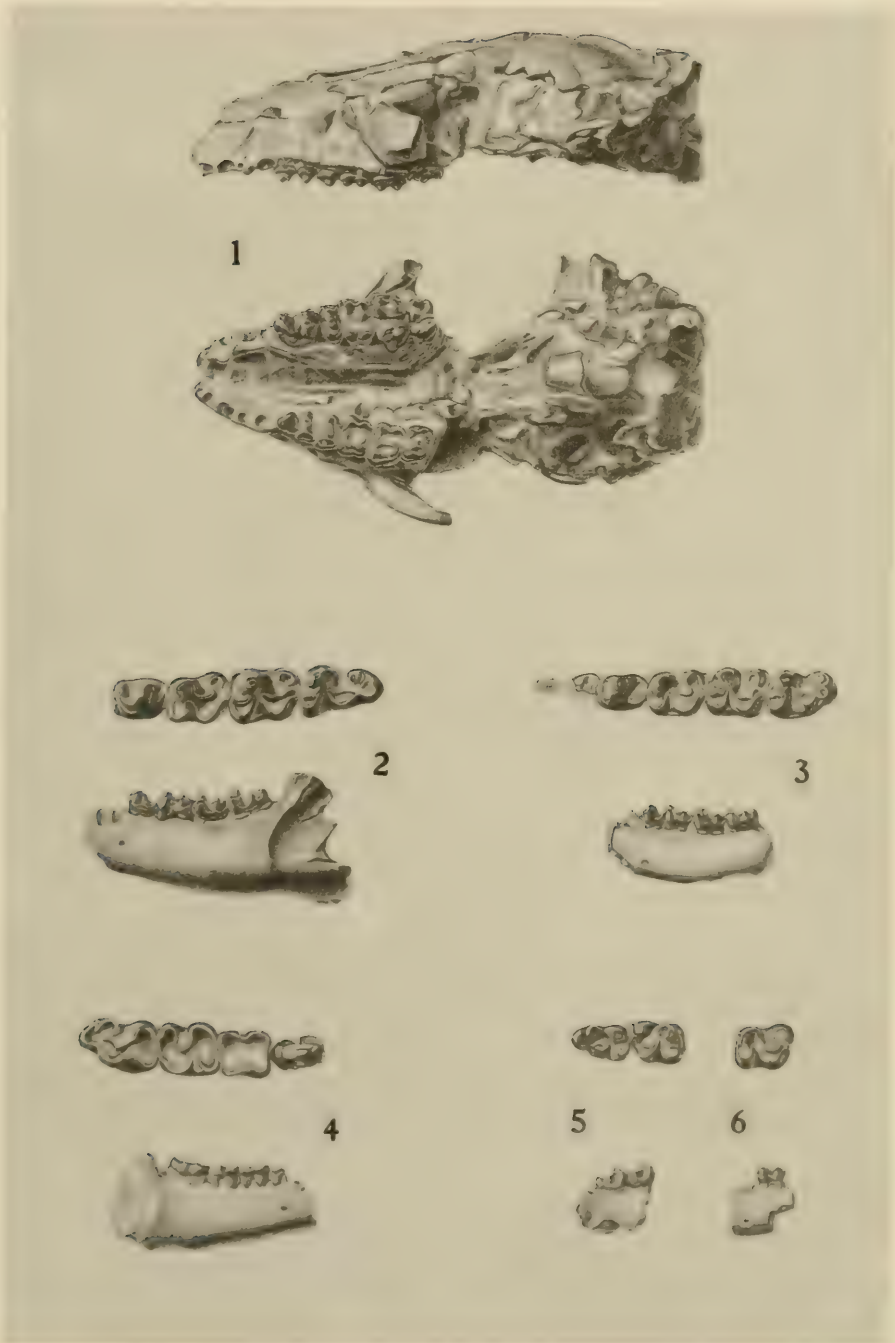


Hyopsodus skull portion and endocranial cast from the early Eocene of Wyoming
(See explanations of plates and abbreviations on pp. 83-90.)



Hyopsodus skull portion, endocranial cast, and deciduous teeth from the Eocene of Wyoming

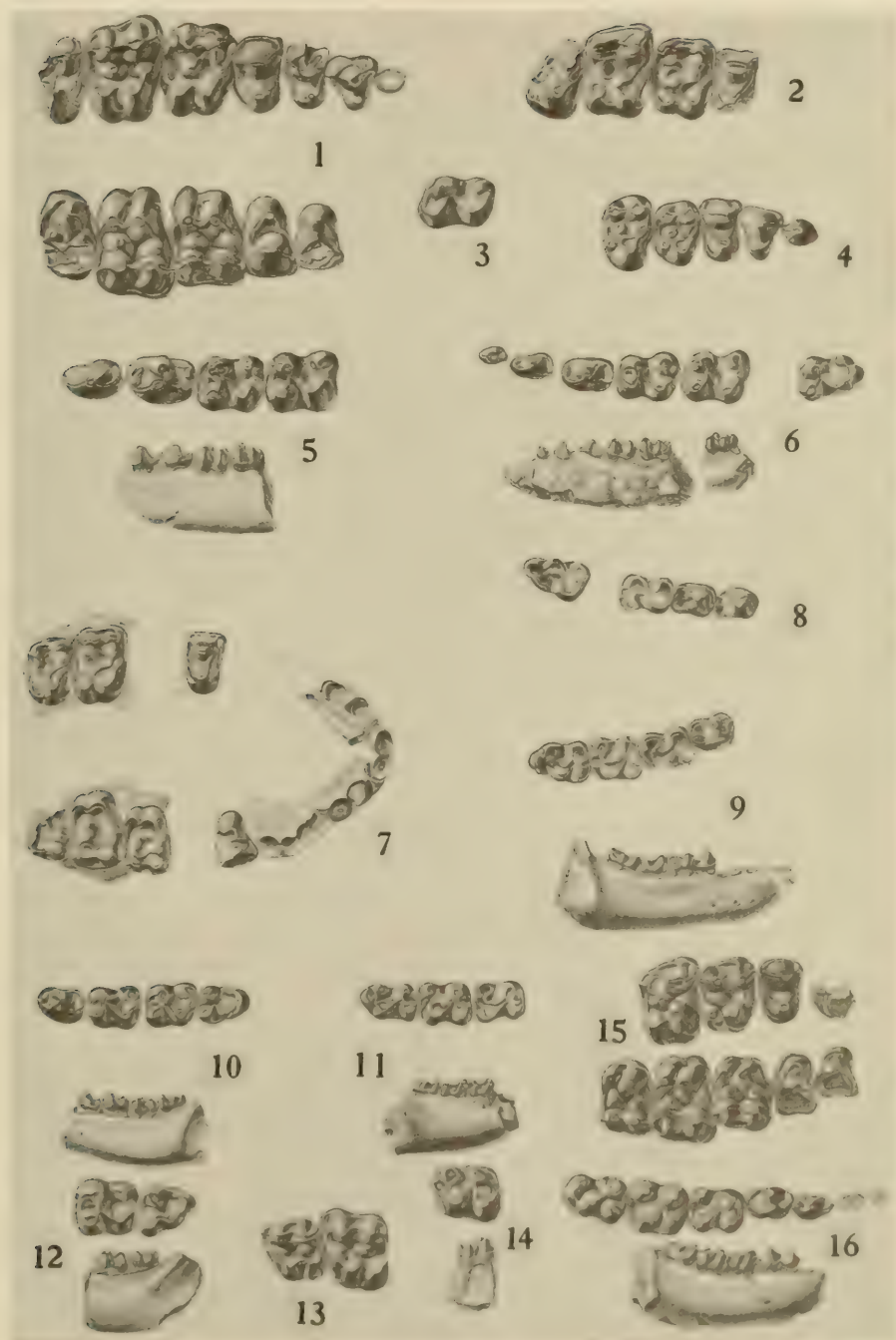
(See explanations of plates and abbreviations on pp. 83-90.)



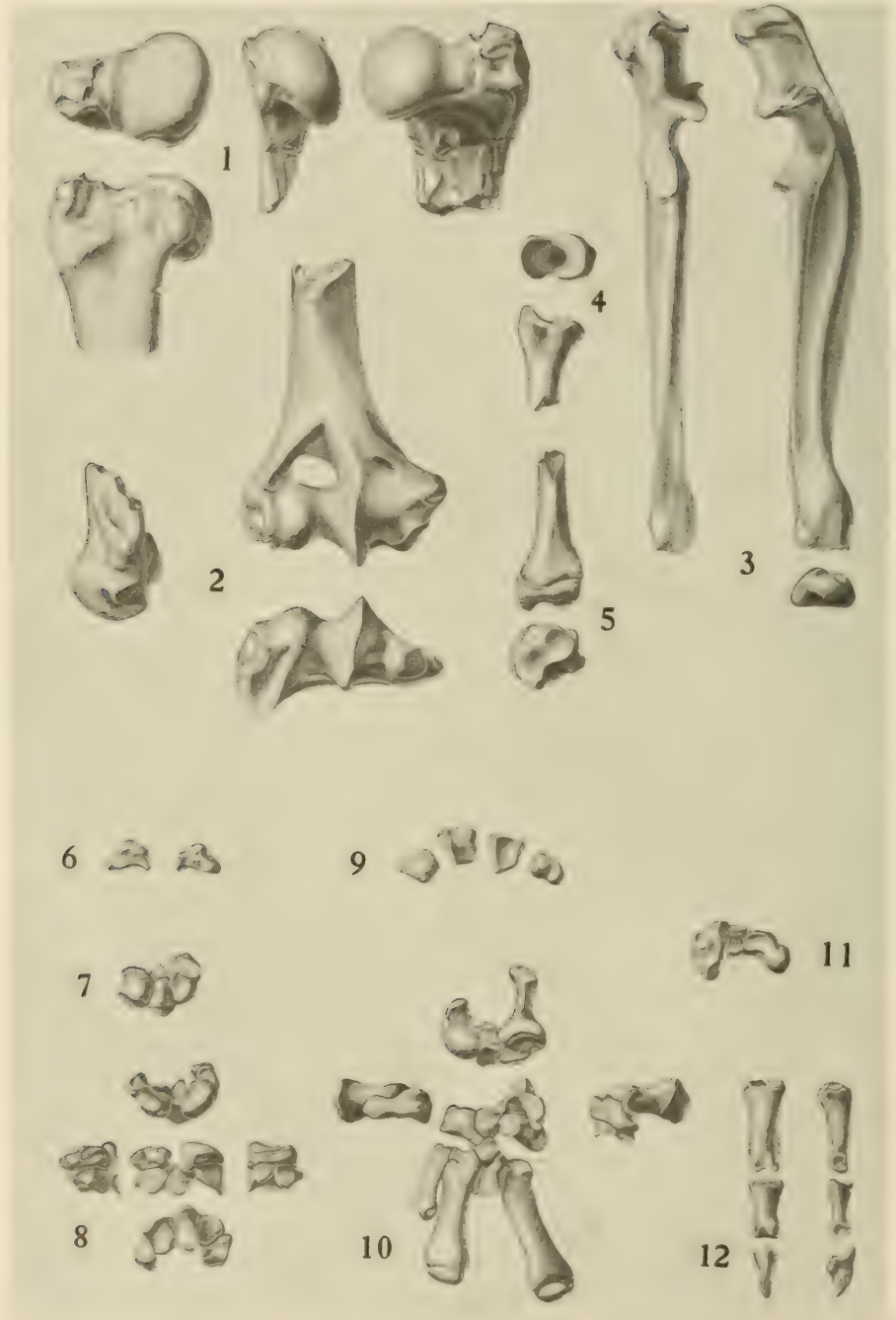
Hyopsodus type-specimens from the middle Eocene of Wyoming
(See explanation of plates on pp. 83-90.)



Hyopsodus type-specimens from the early Eocene of Wyoming
(See explanation of plates on pp. 83-90.)



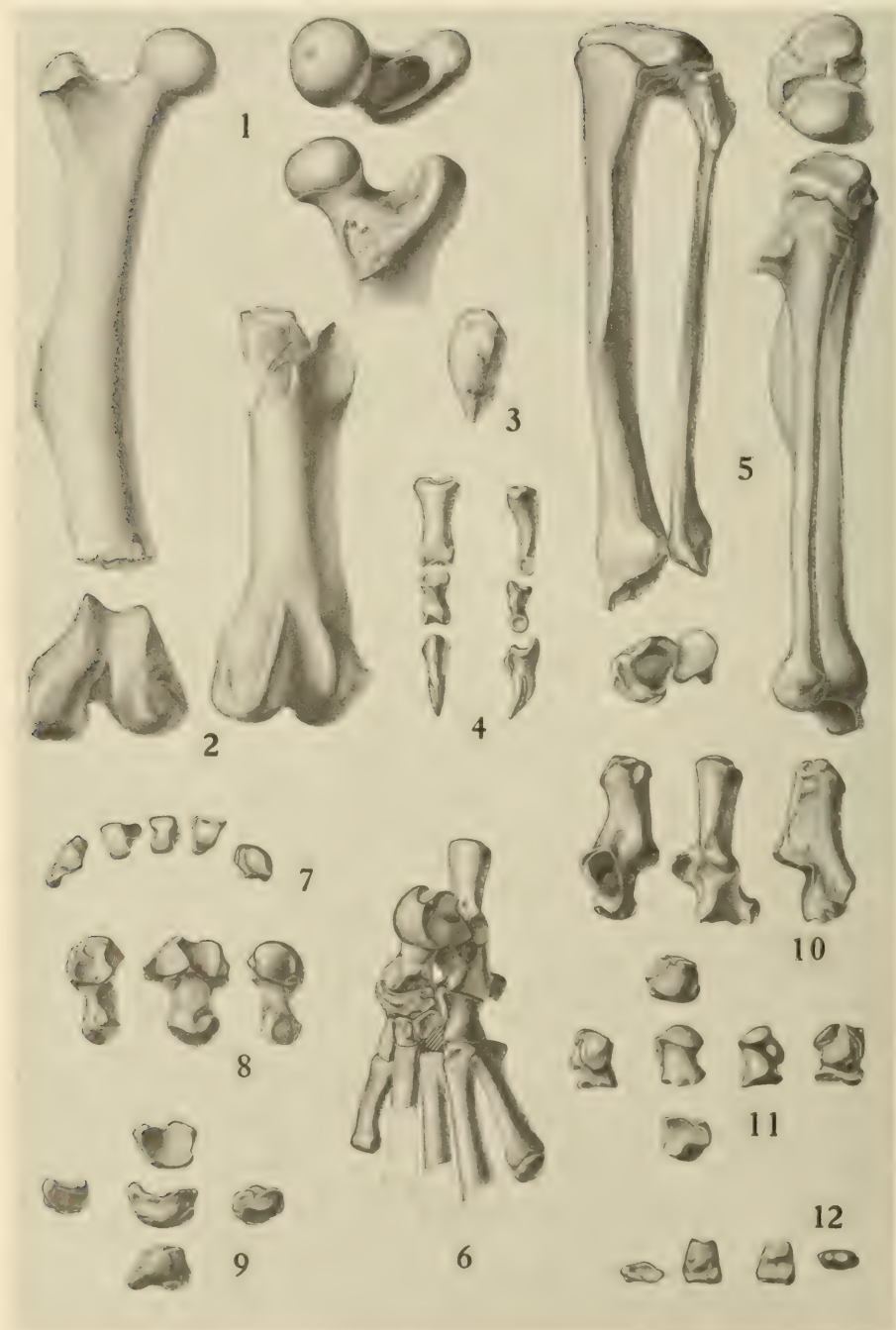
Hyopsodus type-specimens from the early, middle, and late Eocene of Wyoming
(See explanation of plates on pp. 83-90.)



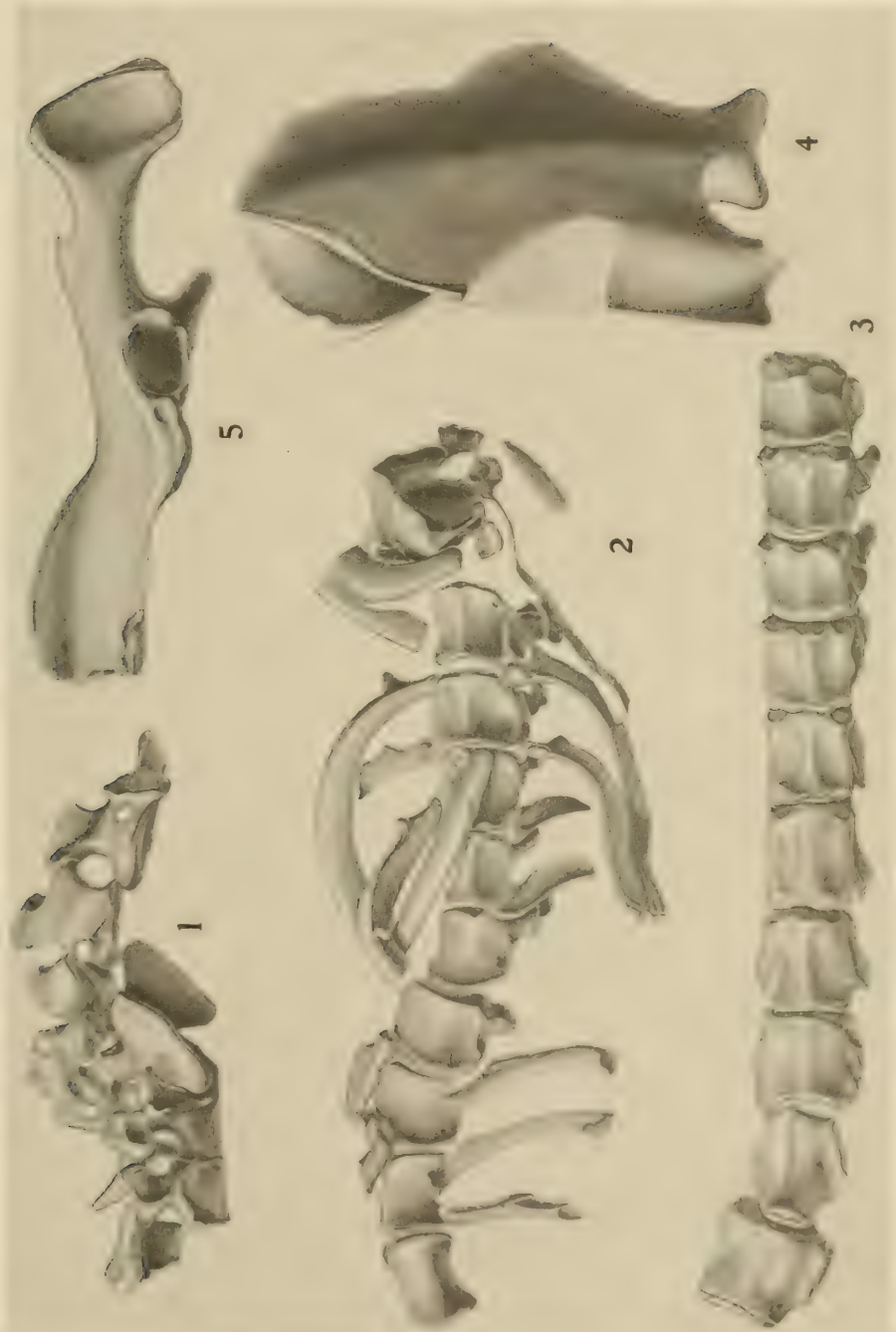
Hyopsodus fore limb and foot material from the middle Eocene of Wyoming
(See explanation of plates on pp. 83-90.)



Hyopsodus skull, fore limb, and foot material from the middle Eocene of Wyoming
 (See explanation of plates on pp. 83-90.)



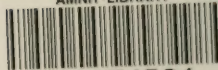
Hyopsodus hind limb and foot material from the middle Eocene of Wyoming
(See explanation of plates on pp. 83-90.)



Hyopsodus vertebrae, ribs, scapula, and pelvis from the middle Eocene of Wyoming

(See explanation of plates on pp. 83-90.)

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